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PARASITOLOGY

EDITED BY

GEORGE H. F. NUTTALL, F.R.S.

QUICK PROFESSOR OF BIOLOGY IN THE UNIVERSITY OF CAMBRIDGE

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GEORGE H. F. NUTTALL, M.D., Ph.D., Sc.D., F.R.S.

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ANTONY VAN LEEUWENHOEK

1632—1725

PORTRAITS

Commencing with *Parasitology*, vol. XIII, No. 1, the Editor proposes to publish a series of portraits of those who have advanced the subject of Parasitology by their researches. Each number of the Journal will be accompanied by one or two portraits serving as frontispieces. The portraits will not be issued in any particular order.

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The last number of each volume will contain brief notes bearing on the subjects of the portraits.

G. H. F. NUTTALL.

VOLUME XIII MARCH, 1921 No. 1

ON TWO NEW TAPEWORMS FROM THE OSTRICH, WITH A KEY TO THE SPECIES OF *DAVAINEA*.

BY F. J. MEGGITT, M.SC., PH.D.
Assistant Helminthologist, University of Birmingham.

(*From the Research Department in Agricultural Zoology, University of Birmingham.*)

(With Plate I and 2 Text-figs.)

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THE material which forms the basis of the following account consists of two tubes of tapeworms collected from ostriches at the Veterinary Pathological Laboratory, Nairobi, British East Africa. One tube contained approximately 12 scolices and the anterior portions of the strobilae attached to them, together with several fragments of the more posterior portions: these are described under the name *Davainea beddardi* n. sp. The other tube contained one large fragment of a *Davainea* and several smaller pieces but no scolices: these are described under the heading *Davainea* sp. For this material I am indebted to Professor G. H. F. Nuttall, F.R.S. to whom I wish here to express my thanks. I have also to acknowledge my indebtedness to the Librarian of the Royal College of Veterinary Surgeons for allowing me to consult literature unobtainable elsewhere.

Davainea beddardi n.sp.

The length of the largest fragment was 6·4 mm. and the greatest breadth observed 3 mm.

The scolex (Plate I, fig. 2) is 1·3 mm. diameter, possessing four unarmed suckers and a rostellum bearing a double row of approximately 130 hooks, each 0·085–0·088 mm. long and of the typical *Davainea* shape, the two rows of

hooks exhibiting a rather irregular alternation of large and small forms. The rostellum itself consists of a short broad central portion, 0·48 mm. diameter, bearing the hooks, surrounded by a band of parenchymatous tissue, 0·81 mm. diameter, in shape like a pneumatic tyre, the whole bearing a remarkable resemblance to the scolex (Plate I, fig. 1) of *Davainea brotogerys* Meggitt, 1915. This appearance has been figured by Zilluf (1912, 17) for a form he calls *Davainea struthionis* but which is instead probably identical with *D. beddardi*. With the exception of the armed collar posterior to the rostellum, figured by Dujardin (1845, Plate 9, fig. LI) and mentioned by Stossich (1895) and Blanchard (1891 *a*, 435) for *D. frontina* (Duj.), in no other species of *Cotugnia* or *Davainea* has this modification of the scolex been mentioned, and absence of comment in the case of so noticeable a structure must be held to imply the absence of the structure itself. It is impossible for this appearance to have been caused by the method of fixation or for it to be a temporary character in any way. It was characteristic of each of the 12 scolices of *D. beddardi* and all those of *C. brotogerys*, although the two forms were fixed by different reagents. The close similarity of the two scolices is interesting in view of the fact that one genus has a double and the other only a single set of genital organs in each proglottis, and forms yet another comment, if one were needed, upon the inadvisability of distinguishing species by the size and external appearance of the scolex alone unaccompanied by any internal morphological difference. A neck is absent. All proglottides seen were broader than long: in those containing mature eggs the length approximated to the breadth.

The longitudinal musculature (Plate I, fig. 3) is arranged in two layers, a stronger internal one of numerous bundles of small fibres and a weaker external one, often absent, of isolated fibres. Separating these two is a thin layer of transverse muscles, while a second band exists internally to the inner longitudinal muscle layer. In the extreme anterior portion of the strobilus (Plate I, fig. 4), the two longitudinal muscle layers merge into one, the separating transverse muscles disappearing. The genital pore is unilateral opening at the posterior two-thirds of the proglottis margin. There is a deep narrow genital cloaca at the bottom of which open the genital ducts. Both male and female ducts pass dorsal to the longitudinal excretory vessels. The cirrus-sac is small, not extending beyond the longitudinal nerve-cord and, as far as could be ascertained in the state of preservation of the material, had a very feeble muscular structure. The cirrus is unarmed and that portion of the vas deferens inside the cirrus-sac is coiled several times in the form of a very twisted piece of rope. The coils of the vas deferens stretch from the inner end of the pouch half-way across the proglottis, then break up into the vasa efferentia. Neither vesicula seminalis nor sacculus accessorius could be observed. The testes are small, approximately 100 in number, and fill the whole of the dorsal surface of the proglottis, extending laterally to the longitudinal excretory vessels. Proglottides containing the sexually mature female organs were absent. From the immature segments found, it could be

ascertained that a small spindle-shaped receptaculum seminis is present and that the female glands are posterior and ventral.

The onchospheres, in groups of 5–8, are enclosed in capsules which fill the whole field, extending laterally beyond the longitudinal excretory vessels but not beyond the nerve.

The only species of tapeworm so far recorded from the ostrich belong to the genus *Davainea*. The first mention of any Cestode parasites from this host was by Houttuyn (1773) and Rudolphi (1810 and 1819) who listed under the name of *Taenia struthionis* a form from *Struthio camelus*. Their records were unaccompanied by any description whatsoever, and it was not until the appearance of Parona's paper (1885) that the species mentioned by the two previous authors was given characters which adequately distinguished it. A few years later it was placed by Fuhrmann (1896, 128) in the new genus *Davainea*. In 1893, von Linstow described from *Struthio molybdophanos* forms which he regarded as belonging to this species, but at the same time found certain discrepancies between his own observations and Parona's account. From *Struthio australis* L. (= *S. australis* Gurn.?) Hungerbühler (1910, 511) later described under the name *Davainea struthionis* (Houtt.) cestodes which he believed identical with both Parona's and von Linstow's specimens but which differed from those of the latter in having a rostellum armed with numerous rows of fine thorn-shaped hooks, 0·005 mm. long, in addition to the usual double circle of rostellar hooks. No further investigations, beyond those of Zilluf (1912) on the musculature of the scolex, were made until 1915 when Beddard showed, while describing the anatomy of some *Davaineas* from *Struthio masaicus*, that the descriptions of von Linstow and Parona applied to separate species, thus accounting for the discrepancies mentioned above. His own specimens, he concluded, might or might not be identical with those found by Parona, but were certainly different from those found by von Linstow. Speaking of his own and Parona's forms, he states (p. 601), "If we can trust as differential characters the diameter of the proglottides and the size of the scolex then the two forms are different. There are no other data that seem to permit of a more definite expression of opinion," and on these grounds does not name his specimens. At this time there are thus two well-defined species of tapeworms parasitic in *Struthio*, one from *S. molybdophanos* described by von Linstow, and the other described by Parona and Beddard from *S. camelus* and *S. masaicus* respectively. Hungerbühler's specimens from *S. australis* agree best with those described by von Linstow, the scolex and cirrus-sac being of approximately the same size, while the characters in which they differ, the presence of a rostellum and its additional armature, are such as would not be apparent in poorly preserved specimens and so may possibly have been overlooked by von Linstow.

From the first of these two species the form found at Nairobi differs in the presence of calcareous corpuscles and of a rostellum, in the absence of pigment in the scolex, in the shape of the hooks and in the length of the

cirrus-sac: from the second it is distinguished by having the eggs enclosed in groups in capsules. Neither does it agree with any of the species of *Davainea* previously described from other hosts. For its reception therefore, there must be formed a new species, for which I suggest the name *Davainea beddardi* n. sp. after Dr Beddard whose paper has largely dissipated the confusion formerly associated with Parona's *D. struthionis*. The following table gives the characters in which the three species differ one from the other.

	Davainea struthionis Parona	*Davainea struthionis* v. Linstow	*Davainea beddardi* n. sp.
Scolex	2 mm. diam. quadrate Parona 1·2 mm. diam. Beddard	1·125–1·18 mm. diam.	1·3 mm. diam. globular
Rostellum	present	absent (?)	present
Rostellar hooks (for shape see Text-fig. 1)	130, 0·02–0·03 mm. long	164, 0·075–0·084 mm. long	130, 0·085–0·088 mm. long
Suckers	non-pigmented	pigmented	non-pigmented
Calcareous corpuscles	present in scolex	absent from scolex	present in scolex
Cirrus-sac	reaches nerve cord	reaches ventral longitudinal excretory vessel	reaches nerve cord
Genital pore	in anterior part of proglottis margin		in posterior part of proglottis margin
Eggs	singly in capsules	capsules contain 8–12	capsules contain 5–8
Host	*S. camelus* *S. masaicus*	*S. molybdophanos*	*S. masaicus*

In order that confusion may not be caused by the use of the same name for two separate species, I venture to separate von Linstow's form from Parona's under the name of *Davainea linstowi* and to give a diagnosis of the specific characters of each of the three species of tapeworms so far recorded from the ostrich. These characters include those mentioned by Dr Beddard and others taken from the original drawings and descriptions.

D. struthionis (Parona, 1885).

Length 270 mm., greatest breadth of proglottides 8·5–9 mm. Scolex 2 mm., diam., quadrate, with rostellum bearing a double circle of hooks 0·02–0·03 mm. long, the shorter and larger hooks alternating. Suckers unarmed. Genital pores unilateral, anterior. Cirrus-sac reaching to nerve-cord. Ova 0·03 mm. long × 0·02 mm. broad, singly in egg-capsules extending laterally to ventral longitudinal canal.

HOST. *Struthio camelus* L., *S. masaicus* Neu.

LITERATURE. Parona, 1885 (*Taenia struthionis*).
Beddard, 1915 (*Davainea struthionis*).
Blanchard, 1891 (*Davainea struthionis*).

D. linstowi n. sp.

Length 160–620 mm., greatest breadth of proglottides 4·43 mm. Scolex 1·18 mm. diam., armed with 164 hooks, 0·084–0·075 mm. long, in two rows, the

longer and shorter forms alternating. Rostellum absent (?). Suckers unarmed, pigmented. Calcareous corpuscles absent anteriorly. Genital pores unilateral, posterior. Cirrus-sac reaches ventral excretory canal. Ova 0·052 mm. diam., 8–12 in each capsule.

HOST. *Struthio molybdophanos* Reichen, *S. australis* Gurn.
LITERATURE. von Linstow, 1893 (*Taenia struthionis*).
Blanchard, 1899*a* (*Davainea struthionis*).
Hungerbühler, 1910 (*Davainea struthionis*).

D. beddardi, n. sp.

Length ? , greatest breadth of proglottides 3 mm. Scolex 1·3 mm. diam., globular, with rostellum armed with 130 hooks 0·085–0·088 mm. long, in two rows. Suckers unarmed. Calcareous corpuscles numerous in scolex. Genital pores unilateral, posterior. Cirrus-sac reaching to nerve-cord. Ova in groups of 5–8 in capsules extending laterally to ventral longitudinal canal.

HOST. *S. masaicus.*
LITERATURE. Present paper.
Zilluf, 1912 (*Davainea struthionis*).

Davainea sp.

The scolex and anterior portion of the strobilus were not seen. The inner longitudinal musculature (Plate I, fig. 5) consists of two layers, an inner and an outer, separated by a band of very weak transverse muscles. The inner longitudinal muscles form a single row of bundles, each composed of many (25–40) separate fibres; in some cases the bundles are entirely distinct one from the other, in others so crushed together that they appear as one continuous layer. Normally there is a certain amount of intermingling but the limits of the individual bundles can usually be ascertained. This layer is bounded internally by a strong band of transverse muscles. The outer longitudinal muscle layer is much weaker and the bundles more scattered than is the case with the inner. Its inner limit is formed by scattered bundles invariably distinct one from the other and consisting of but few fibres (3–6). From this, smaller bundles and isolated muscle strands are strewn through the cortex to the limits of the cuticula, the stronger muscle groups being the more internal and the fibres becoming successively weaker the more they approach the cuticula. In addition to these layers, a plate of dorso-ventral fibres separates each proglottis from its neighbours.

The excretory system consists of two longitudinal vessels only, united posteriorly in each proglottis by a commissure. Dorsal longitudinal vessels could not be seen.

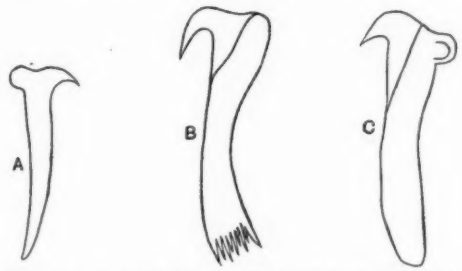
The genital pore (Plate I, fig. 7) is unilateral, at the posterior three-quarters of the proglottis margin. The genital cloaca is comparatively shallow and leads diagonally and anteriorly into the proglottis. The cirrus-sac is long and slender, only reaching to the nerve-cord, and of very feeble muscular

structure. It runs diagonally nearly to the anterior border of the proglottis and at approximately two-thirds of its length makes a right-angled turn towards the dorsal surface. The cirrus is short, uncoiled, and unarmed, and opens into the vas deferens while still only half-way along the cirrus-sac. After a few coils which fill up the remainder of the cirrus-sac, the vas deferens emerges from the inner extremity and extends as a coiled duct along the antero-dorsal surface of the proglottis to a point half-way between the excretory vessels, there splitting up into the vasa efferentia. The testes are numerous, approximately 200 in number and of normal size. They fill the whole dorsal surface of the proglottis, extending laterally to the longitudinal excretory vessels, but with fewer on the poral side than on the aporal. In the centre of the proglottis, the layer is two or sometimes three testes deep, towards the lateral margins only one deep.

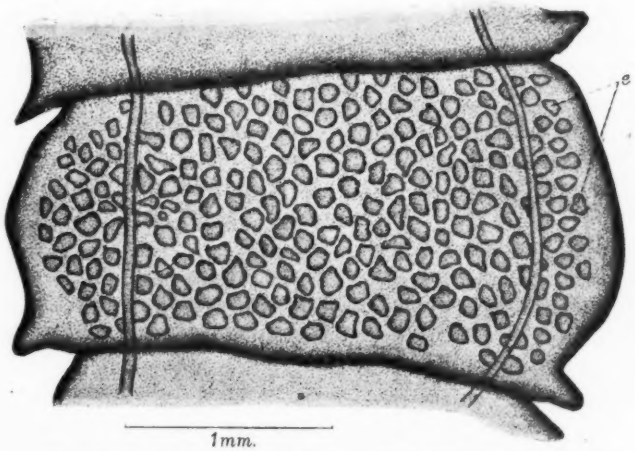
The vagina is devoid of a sphincter muscle. It runs posteriorly to the cirrus-sac and then proceeds transversely across the proglottis, midway between the dorsal and ventral surfaces, passing the excretory vessels. At one-third of the proglottis breadth it opens into the receptaculum seminis. This latter is a narrow thin-walled tube gradually decreasing in diameter as it approaches the centre of the proglottis. It is always choked with spermatozoa. The ovary is a comparatively small but very much lobed gland, lying on the ventral surface of the proglottis with the lobes directed towards the dorsal surface; its ventral aspect is flat. It lies ventral and slightly posterior to the inner end of the receptaculum seminis. Posteriorly to it and of a slightly smaller size is the yolk-gland. This is bilobed, with the two lobes united by a narrow bridge from which springs the vitelline duct. It is more compact than the ovary. The shell-gland is in the form of a sphere of cells united at their inner extremities and grouped round the oviduct, and lies upon the dorsal surface half-way between the yolk-gland and ovary. Inside it the oviduct coils slightly before receiving the vitelline duct. A definite but ephemeral uterus is developed, lying transversely across the proglottis, anteriorly to the female glands and inserting itself among the testes on the dorsal surface. It never passes beyond the stage of a small tube, slightly enlarged where the oviduct joins it, and quickly breaks up into egg-capsules, approximately 140 in number, which fill the whole proglottis, extending laterally beyond the longitudinal excretory vessels (Text-fig. 2). Each capsule usually contains six eggs, and is polygonal in shape owing to compression by its neighbours. The interior (Plate I, fig. 6) is filled with a fibrous mass in which the eggs are embedded and which is further partially sub-divided by a dark homogeneous substance similar in appearance to the capsule wall. There is no tendency to isolate separate eggs in the capsule, the partial compartment formed sometimes containing several eggs and sometimes being empty. Also no case could be seen in which the eggs appear each in a separate capsule or scattered through the parenchyma as in other species of *Davainea*. The capsule is far too definite

for it to be a temporary structure or for it to be split up into secondary capsules as in *D. polycalceola* Jan. A similar case has been described by Mola (1907 *a*, p. 578) for *D. hertwigi*: "La vasta cavità uterina è subdivisa imperfettamente in numerosa e piccole cellette, da tessuto parenchimatoso, nelle quali si trovano le uove in numero di 1–3 con le larve esacante."

In comparing this species of *Davainea* with others, the one it most resembles is the previously described *D. beddardi*. In both species the unilateral



Text-fig. 1. Rostellar hooks of Cestodes from the ostrich. *a*, after Parona; *b*, after von Linstow; *c*, author's figure.



Text-fig. 2. Proglottis of *Davainea* sp., filled with egg-capsules (*e*).

genital pores are situated posteriorly along the proglottis margin, the capsules each contain approximately the same number of eggs and extend laterally beyond the longitudinal excretory vessel, and the relative length of the cirrus-sac (only reaching the nerve-cord) is the same. On the other hand they differ markedly in outward appearance and width of the proglottides, in the number of testes—*D.* sp. having approximately twice as many as *D. beddardi*—and in the cirrus-sac being further posterior in the former than in the latter.

A dorsal longitudinal vessel was observed in *D. beddardi*, but could not be found in the other form. The musculature in the former is also distinctly weaker and more diffuse than in the latter, while at the same time not extending so far into the cortex. These differences appear to indicate the existence of two separate species. Considering however that the scolex of the one form is unknown, that the definition of the other was drawn up from fragments, and that both came from the same species of host, the differences above enumerated are certainly not sufficient to justify the creation of two separate species for the two forms. It therefore seems best to leave this form unnamed until its scolex or more complete specimens of *D. beddardi* be found.

The Genus Davainea.

The genus *Davainea* was erected by Blanchard and Railliet in 1891 for the reception of Cestodes characterised by the possession of T-shaped rostellar hooks, armed suckers, and the absence of a persistent uterus. In the same year Blanchard (1891 *a*, p. 429) defined it as follows: "Vers de taille petite ou moyenne. Tête arrondie, surmontée d'un rostre ou creusée d'un infundibulum, mais armée dans l'un et l'autre cas d'une double coûronne de crochets nombreux, petits et d'une forme speciale. Ventouses arrondies, entourées de plusieurs rangées de petits crochets ou spicules, caducs ou persistant pendant toute la vie. Pores génitaux unilatéraux ou irrégulièrement alternes. Dans l'anneau mûr, d'ordinaire beaucoup de corpuscules arrondis, séparés les uns des autres et formés d'un grand nombre d'œufs conglomérés, dépourvus d'appareil piriforme; parfois aussi, œufs isolés, épars dans le parenchyme de l'anneau. Développement inconnu; on suppose que la larve de certaines espèces vit dans la cavité générale des Myriapodes et des Mollusques terrestres. Le Ver adulte est parasite de l'intestine grêle des Oiseau (Coureurs, Gallinacés, Pigeons) et même de l'Homme." The number of species to be assigned to it was estimated by that author as 14, or possibly 16. Fuhrmann (1896, p. 127) later increased that number to 23—two of which however [*D. tauricollis* (Chap.) = *Chapmania tauricollis* (Chap.) and *D.* (?) *clavulus* (v. Lins.) = *Biuterina clavulus* (v. Lins.)] are now placed in other genera—but "Von diesen 23 Vertretern des Genus *Davainea* sind nur 10 anatomische genauer untersucht." Since that date our knowledge of the genus has been increased greatly, largely owing to the work of the last named author, until in 1908 the number of species of *Davainea* from birds amounted to 59, collected from 74 hosts (Fuhrmann, 1908). To this number must be added 31 others described in the last ten years which, together with the 16 species from mammals not listed by him, increases the total number to 106 from 120 hosts.

The genus itself may now be defined as *Taenioidea*:

Scolex with simple rostellum armed with a double row of very numerous and generally very small hammer-shaped hooks. Suckers armed or unarmed[1].

[1] Both Ransom (1909, p. 67) and Fuhrmann (1908, p. 42) omit to state in their diagnoses of the genus that the suckers are sometimes unarmed (*e.g. D. cesticillus* Mol.).

A single set of reproductive organs in each segment. Genital pores unilateral or alternating[1]. Uterus persistent (*D. uterina* Fuhr.), or transient: in the latter case the eggs are either enclosed in egg-capsules or are scattered throughout the parenchyma (*D. rhynchota* Rans.). Eggs with thin transparent shells. Adults in mammals or birds. Larval stage a cysticercoid parasitic in molluscs or insects. Type species—*Davainea proglottina* (Davaine, 1860).

The species of the genus fall roughly into four classes, the division being based upon the armature of the suckers, and the position of the genital pores.

Aa. Genital pores unilateral, suckers armed.
Ab. Genital pores unilateral, suckers unarmed.
Ba. Genital pores alternating, suckers armed.
Bb. Genital pores alternating, suckers unarmed.

This division, while useful for dealing with a large number of species and for identification, cannot be regarded as wholly natural. The armature of the suckers is very transient and many of the species at present said to possess unarmed suckers may, when their life-histories are fully known, be found to lose their acetabular hooks at an early stage. Neither is the position of the genital pores a character altogether suitable for the characterisation of subgenera. *D. tetragona* (Mol.) possesses unilateral genital pores and *D. echinobothrida* (Még.) alternating pores in the adult form and unilateral in the young. The two species are closely related and no classification can be regarded as satisfactory which separates them. A character upon which a classification may perhaps be finally based is the behaviour of the uterus and the origin of the egg-capsules. A large number of species have egg-capsules each containing only one egg (*e.g. D. cesticillus* Mol., *D. corvina* Fuhr., *D. microcotyle* Skrj.), others possess from two (*D. celebensis* Jan., *D. friedbergi* Lins.) to 14 or 15 eggs per capsule (*D. oligorchidna* Fuhr., *D. salmoni* Stiles): in *D. insignis* Steudener (1877, p. 302)—"Der Uterus dehnt sich dann mehr und mehr aus und bildet schliesslich einen die ganze Mittelschichte des Gliedes einnehmenden Sack, in welchen die Eier durch eine körnige Substanz zu Conglomeraten verbunden sind," and in *D. uniuterina* (Fuhrmann, 1909, p. 114)—"Der Uterus scheint sich nicht (oder sehr spät) in einselne Parenchymkapseln aufzulösen, sondern als einheitlicher, stark gelappter Uterus bestehen zu bleiben," while in *D. rhynchota* Ransom (1909, p. 14), distinctly states that the eggs are scattered singly throughout the parenchyma and are not enclosed in capsules. Beddard (1914, pp. 875 and 885) again considers the egg-capsules as formed by a number of parauterine organs. Unfortunately our knowledge of the behaviour of the uterus in this genus is not sufficiently extensive to allow of the utilisation of this character. Its structure and behaviour in many of the species are entirely unknown and in others but insufficiently described. All our knowledge of *D. difformis* (Rud.) is contained in a statement by Fuhrmann (1908, p. 45), "Rudolphi nannte diese Art

[1] Ransom (*loc. cit*) states the genital pores *occasionally* alternate.

T. difformis Rud. 1819; sie ist, wie er selbst sagt, identisch mit *Taenia brevicollis* Frölich. In der Rudolphischen Sammlung finden sich in Glas No. 1906 die Typen dieses Cestoden, deren Untersuchung gezeigt, dass es ein Vertreter des Genus *Davainea* ist. Ich behalte den Namen, zu welchem die Typen existieren, bei." *D. globocephala* Fuhr., *D. circumcincta* (Krabbe), *D. longicollis* (Mol.) are equally unknown, while of *D. australis* (Krabbe) only the armature of the head has been described. Under these circumstances any classification based upon characters other than those usually given (armature of scolex, position of genital pore) must of necessity exclude large numbers of species. I have therefore sub-divided the genus into the four divisions given above as the best available means of separating the greatest number of species into distinct classes with a view to facilitating identification and systematic manipulation. The classification of birds follows that of Sharp in the British Museum Handbook of Birds. The references given are other than are to be found in Fuhrmann's *Die Cestoden der Vögel.*

LIST OF SPECIES OF DAVAINEA AND THEIR HOSTS.

Mammalia.

PRIMATES.

Homo sapiens L.

D. asiatica (von Linstow, 1901); 1901 *a*, 982; 1901 *b*, 283.

D. formosana Akashi[1], 1917.

D. madagascariensis[2] (Davaine, 1870); Blanchard, 1891 *a*, 438; 1891 *b*, 613; 1897, 34; 1899 *a*, 200 and 215. Chevreau, 1891, 523. Davaine, 1877, liii and 922. Daniels, 1895; 1896, 1455. Grenet and Davaine, 1869, 233; 1870, 134. Holzberg, 1898, 174. Leuckart, 1891, 68. v. Linstow, 1901 *a*, 984. Parona, 1898, 106. Stevens, 1916, 329. Stiles, 1896 *b*, 55.

Galeopithecus volans.

D. lateralis Bourquin, 1906, 222.

RODENTIA.

Arvicanthys abyssinicus.

D. polycalceola v. Janicki, 1902. Parona, 1909, 2.

Arvicanthys pumilis Sparrm. var. *bechanae.*

D. trapezoides v. Janicki, 1904. Hungerbühler, 1910, 516.

Geomys breviceps Baird.

D. sp. Douthitt, 1915.

RODENTIA—*continued.*

Lepus arizonae.

D. retractilis Stiles, 1895. Stiles, 1895; 1896, 195. Blanchard, 1899 *a*, 207 and 215. Parona, 1898, 106.

Lepus melanotis.

D. salmoni Stiles, 1895. Stiles, 1895; Stiles, 1896, 198. Blanchard, 1899, 207 and 214.

Lepus sylvaticus.

D. salmoni Stiles, 1895. Stiles, 1896, 198. Blanchard, 1899 *a*, 207 and 214. Parona, 1898, 106.

Mus flavidus.

D. (?) *gracilis* v. Janicki, 1904, 779; 1906, 570.

Mus meyeri.

D. celebensis v. Janicki, 1902, 275.

Mus muschenbrocki.

D. polycalceola v. Janicki, 1902, 258; 1906, 543. Parona, 1909, 2.

Mus rajah.

D. blanchardi (Parona, 1898). Blanchard, 1899 *a*, 210 and 216. Parona, 1898, 103.

[1] If the rostellar hooks be thorn-shaped, this is more probably a *Dipylidium.*

[2] Synonym: *Taenia demarariensis* Daniels, 1895.

RODENTIA—*continued.*

Mus siporanus.

D. blanchardi (Parona, 1898). Blanchard, 1899 *a*, 210 & 216. Parona, 1898, 103.

Mus variegatus.

D. trapezoides v. Janicki, 1904, 779; 1906, 568. Hungerbühler, 1910, 516.

INSECTIVORA.

Erinaceus albiventris.

D. voluta[1] (v. Linstow, 1904). v. Linstow, 1904 *b*, 381. v. Janicki, 1906, 543.

INSECTIVORA—*continued.*

Erinaceus sp.

D. parva[2] v. Janicki, 1904, 774; 1906, 540.

EDENTATA.

Manis pentadactyla.

D. contorta Zschokke, 1895, 634. Blanchard, 1899 *a*, 215. Parona, 1898, 106. Stiles, 1896, 195.

Aves.

ACCIPITRIFORMES.

Buteo desertum (Daud.).

D. sphaeroïdes Clerc, 1902.

Buteo menetriesi Bogd.

D. sphaeroïdes Clerc, 1902.

Entolmaëtus fasciatus (Vieill.).

D. hertwigi Mola, 1907.

ANSERIFORMES.

Anas bochas domesticus.

D. anatina[3] Fuhrmann, 1909. Lühe, 1910, 52. Skrjabin, 1914 *a*, 68. Stiles, 1896 *b*, 53.

? *D. crassula* (Rudolphi, 1919), Clerc non Fuhrmann. Stiles, 1896 *b*, 53.

D. microcotyle Skrjabin, 1914 *a*, 69.

Anas sp.

D. cyrtus Skrjabin, 1914 *a*, 67.

APTERYGIFORMES.

Crypturus noctivagus (Neu.).

D. crypturi Fuhrmann, 1909.

Crypturus sp.

D. capillaris Fuhrmann, 1909.

Nothura media (Spix.).

D. elongata Fuhrmann, 1909.

Rhynchotus rufescens (Temm.).

D. elongata Fuhrmann, 1909.

D. oligocantha Fuhrmann, 1909.

APTERYGIFORMES—*continued.*

Tinamus sp.

D. elongata Fuhrmann, 1909.

D. oligocantha Fuhrmann, 1909.

ARDEIFORMES.

Garzetta garzetta (L.).

D. circumcincta (Krabbe, 1869). Blanchard, 1899 *a*, 215.

CASUARIIFORMES.

Casuarius uniappendiculatus Blyth.

D. sp. nov. Vevers, 1920, 408.

D. sp. nov. Vevers, 1920, 408.

Dromaeus novae-hollandiae Lath.

D. australis (Krabbe, 1869). Blanchard, 1899 *a*, 215. Johnston, 1912, 106. Stiles, 1896 *b*, 54.

CHARADRIIFORMES.

Himantophus leucocephalus Gould.

D. himantopodis Johnston, 1911. Johnston, 1911, 75; 1912, 107.

Totanus fuscus (L.).

D. minuta Cohn, 1901. Lühe, 1910, 52.

COCCYGES.

Chrysococcys klassi (Steph.).

D. sp.[4] Parona, 1909.

[1] Considered by v. Janicki (1906, p. 543) as possibly identical with his own species *D. parva*.

[2] This species, together with the closely allied *D. voluta* (v. Linstow), is placed by Janicki (1906, p. 543) in the genus *Davainea*, but the absence of hooks on the scolex, the passage of the genital canals dorsal to the nerve and excretory vessels, the position of the testes lateral and posterior to the female organs, and the enclosure of the eggs single in egg-capsules seem rather to refer it to the genus *Oochoristica*.

[3] Synonyms: *D. crassula* (Rud.) Wolffhügel, 1899.

[4] This species is considered by Parona (1909) as possibly identical with *D. differmis* Rud. or *D. mutabilis* Rüther.

COCCYGES—*continued.*

Corythaeola cristata (Vieill.).

D. calcarea Fuhrmann, 1909.

D. undulata Fuhrmann, 1909.

Cuculus canorus L.

D. difformis[1] (Rudolphi, 1819).

Gallerix porphyreolophus (Vig.).

D. leptosoma (Diesing, 1850).

Schizorhis concolor (Smith).

D. sp. inq. Vevers, 1920, 408.

Turacus buffoni (Vieill.).

D. macroccirrosa Fuhrmann, 1909. Skrjabin, 1914 *a*, 70.

COLUMBRIFORMES.

Caloenas nicobarica (L.).

D. paucitesticulata Fuhrmann, 1909. Vevers, 1920, 408.

Columba livia Bonn.

D. crassula[2] (Rudolphi, 1819). Fuhrmann non Clerc. Blanchard, 1899 *a*, 215. Fuhrmann, 1909, 104. Krabbe, 1869, 345; 1879, 15. ? Stossich, 1895, 43.

D. crassula[2] (Rudolphi, 1819). Clerc non Fuhrmann. Blanchard, 1891 *a*, 436. Clerc, 1906, 725. Krabbe, 1882, 363; 1879, 15. Railliet, 1893, 306. Stiles, 1896 *b*, 53.

Columba palumbus L.

D. columbae Fuhrmann, 1909.

Columba sp.

D. cryptacantha Fuhrmann, 1909.

D. spiralis Baczynska, 1914, 198.

Globicera oceanica (Less.).

D. insignis (Steudener, 1877).

Goura albertisi Salvad.

D. goura Fuhrmann, 1909.

COLUMBRIFORMES—*continued.*

Goura coronata (L.).

D. goura Fuhrmann, 1909. Vevers, 1920, 408.

Leucosarcia picata (Lath.).

D. sp. Johnston, 1912, 106.

Turtur decipiens (Fin. and Hartl.).

D. cryptacantha Fuhrmann, 1908.

Turtur turtur (L.).

D. crassula[2] (Rudolphi, 1819). Clerc non Fuhrmann. Blanchard, 1891 *a*, 436. Stiles, 1896 *b*, 53.

D. micracantha Fuhrmann, 1909.

CORACIIFORMES.

Buceros seratogynia.

D. emperus Skrjabin, 1914 *a*, 69.

Colius leucotis affinis Shell.

D. werneri Klaptocz, 1908, 281. Fuhrmann, 1912, 192.

Podager nacunda (Vieill.).

D. magnicoronata Fuhrmann, 1909. Skrjabin, 1914 *a*, 70.

GALLIFORMES.

Caccabis chukar Gray.

D. nov. sp. Vevers, 1920, 408.

Caccabis petrosa (Gm.).

D. circumvallata (Krabbe, 1869). Mola, 1907 *b*, 126; ? 1912, 440.

Caccabis saxatilis (Wolf and Meyer).

D. crassula (Rudolphi, 1819). Clerc non Fuhrmann. Stiles, 1896 *b*, 53.

D. urogalli[3] (Modeer, 1790). Morell, 1895, 16.

Coturnix coturnix (L.).

D. circumvallata[4] (Krabbe, 1869). ? Mola, 1912, 440. Stiles, 1896 *b*, 47. Stossich, 1895, 42.

[1] Synonym: *Taenia brevicollis* Frolich.

[2] Under the name *D. crassula* (Rud., 1819) two different forms have been described. The description of the one form was by Fuhrmann (1909, p. 104) from the study of Rudolphi's type species and therefore must be regarded as defining the species. The other form described under the name *D. crassula* (Rud) by Stiles (1896 *b*, p. 53), Railliet (1893, p. 306) and Clerc (1906, p. 725), and under that of *D. columbae* (Zed.) by Blanchard (1891 *a*, p. 436) differs from the type species in having unilateral genital pores, armed suckers, and rostellar hooks of half the size of those seen by Fuhrmann. Two species seem thus to have been confused together under the one name. Clerc's form further differs from those seen by Stiles and Railliet in having 400 rostellar hooks instead of 70. Fuhrmann (1908, pp. 74 and 44) considers *Alyselminthus columbae* Zeder (1800) and *Halysis columbae* Zeder (1803) as possible synonyms of *D. crassula* Rud. This Cestode was first described by Rudolphi (1810, p. 94) under the name *Taenia sphenocephala*, but as this, according to Fuhrmann's (1906, p. 449) study of the type species, is a *Hymenolepis*, *Alyselminthus columbae* and *Halysis columbae* cannot possibly be synonyms of *D. crassula.*

[3] Synonyms: *Taenia calva* Baird, 1853; *T. microps* Diesing, 1857; *T. tumens* Mehlis.

[4] Synonym: *Taenia lineata* Rudolphi ex parte.

GALLIFORMES—*continued.*

D. polyuterina Fuhrmann, 1909.

Coturnix communis.

D. circumvallata (Krabbe, 1869). Blanchard, 1891 *a*, 434.

D. pluriuncinata[1] (Crety, 1890). Blanchard, 1891 *a*, 434. Crety, 1890, 10. Fuhrmann, 1908, 43. Mola, 1912, 432. Stiles, 1896 *a*, 47.

Crax alector (L.).

D. leptacantha Fuhrmann, 1909.

Crax fasciolata Spix.

D. leptacantha Fuhrmann, 1909.

Crax sp.

D. leptacantha Fuhrmann, 1909.

Francolinus adspersus Waterh.

D. provincialis v. Linstow, 1909, 75.

Francolinus clappertoni Childr.

D. clavicirrosa Fuhrmann, 1909 *b*, 13.

Gallus gallus domesticus.

D. cantaniana[2] (Polonio, 1860). Blanchard, 1899 *a*, 215; 1899, 480.

D. cesticillus[3] (Molin, 1858). Ackert, 1918, 41. ? Dujardin, 1845, 586. Guberlet, 1916 *b*, 37; 1916 *a*, 232. ? Holzberg, 1898, 182. Krabbe, 1879, 13. Meggitt, 1916, 399. Railliet, 1893, 305. Setti, 1893, 20. Sweet, 1910, 242.

D. cohni Baczynska, 1914, 196.

D. dubius Meggitt, 1916, 391.

D. echinobothrida[4] (Mégnin, 1880). Guberlet, 1916 *b*, 36. Ransom, 1904, 55; 1905, 280.

D. longicollis[5] (Molin, 1858). Ariola, 1900, 432. Blanchard, 1894, 701. Fuhrmann, 1908, 43. v. Linstow, 1878, 123. Railliet, 1893, 329.

D. mutabilis Rüther, 1901.

D. penetrans Baczynska, 1914, 192.

D. proglottina (Davaine, 1860). Blanchard, 1899 *a*, 214. Dujardin, 1843, 342; 1845, 630. Hungerbühler, 1910, 519. Magalhães, 1898, 443. Railliet, 1893, 305. Railliet et Lucet, 1892, 105.

GALLIFORMES—*continued.*

D. proglottina var. *dublanensis* Kowalewski, 1905.

D. tetragona[4] (Molin, 1858). Ackert, 1919, 28. Guberlet, 1916 *a*, 233; 1916 *b*, 34. Setti, 1893, 20. Sweet, 1910, 243. Rátz, 1900, 230.

D. varians Sweet, 1910, 243.

D. volzi Fuhrmann, 1905.

Gallus sonnerati Temm.

D. cesticillus[3] (Molin, 1858).

Lagopus scoticus (Lath.).

D. cesticillus[3] (Molin, 1858). Shipley, 1908, 263; 1909 *a*, 357.

D. urogalli[6] (Modeer, 1790). Shipley, 1908, 264; 1909 *a*, 351; 1909 *b*, 368.

Lyrurus tetrix (L.).

D. retusa Clerc, 1903. Shipley, 1909 *b*, 366.

D. urogalli[6] (Modeer, 1790). Morell, 1895, 16. Shipley, 1909 *b*, 366.

Meleagris gallopavo L.

D. cantaniana[2] (Polonio, 1860). Blanchard, 1899 *a*, 215. Fuhrmann, 1908, 104.

D. cesticillus (Molin, 1858).

Numida meleagris L.

? *D. cantaniana*[2] (Polonio, 1860).

Numida ptilorhyncha Licht.

D. nana Fuhrmann, 1912, 185.

D. numida Fuhrmann, 1912, 182.

D. paucisegmentata Fuhrmann, 1909 *b*, 15.

D. pintneri Klaptocz, 1906. Fuhrmann, 1909 *b*, 12; 1912, 191.

Pavo cristatus L.

D. ceylonica Baczynska, 1914, 190.

Penelope obscura Illig.

D. penelopina Fuhrmann, 1909.

Perdix perdix (L.).

D. globirostris Fuhrmann, 1909.

D. polyuterina Fuhrmann, 1909.

Perdix sp.

D. campanulata Fuhrmann, 1909.

D. circumvallata (Krabbe, 1869).

[1] Synonym: *D. circumvallata* (Krabbe) of Morell, 1895.

[2] Synonym: *D. oligophora* Magalhães, 1898.

[3] Synonym: *Taenia infundibuliformis* Goeze of Dujardin, 1845.

[4] Synonyms: *Taenia botrioplitis* ex parte, *Davainea parachinobothrida* Mag., 1898. For full synonomy and literature see Ransom (1904, p. 64) or (1905, p. 278).

[5] Synonyms: *Dibothrium longicollis* (Molin), *Bothriocephalus longicollis* (Molin), *Bothriotaenia longicollis* (Molin).

[6] See footnote 3, p. 12.

GALLIFORMES—*continued.*

D. laticanalis Skrjabin, 1914 *a*, 66.

Phasianus colchicus L.

D. cantaniana[1] (Polonio, 1860). Fuhrmann, 1908, 104.

D. friedbergi[2] (v. Linstow, 1878). Baczynska, 1914, 200.

Phasianus sp.

D. multicapsulata Baczynska, 1914.

Tetrao urogallus L.

D. globocaudata[3] Cohn, 1900. Cohn, 1900, 95. Neslobinsky, 1911, 436. Shipley, 1909 *b*, 368.

D. urogalli (Modeer, 1790). Morell, 1895, 16. Shipley, 1909 *b*, 368. Cohn, 1900, 95.

Tetraogallus himalayensis Gray.

D. urogalli[4] (Modeer, 1790). Morell, 1895, 16.

GRUIFORMES.

Cariama cristata L.

D. brachyrhyncha (Creplin, 1853).

PASSERIFORMES.

Cacicus affinis Swains.

D. globocephala Fuhrmann, 1909.

Conopophila albigularis (Gould).

D. conopophilae Johnston, 1912, 110.

Corvus coronoides Vig. and Horsf.

D. sp. Johnston, 1912, 112.

Corvus culminatus Sykes.

D. corvina[5] Fuhrmann, 1905. Fuhrmann, 1908, 46; 1911, 251.

Corvus macrorhynchus Wagl.

D. corvina Fuhrmann, 1905

Entomyza cyanotis (Lath.).

D. conopophilae Johnston, 1912, 111.

Fringilla coelebs L.

D. sp inq. Vevers, 1920, 408.

Galerita macrorhyncha Tristr.

D. galeritae Skrjabin, 1914 *a*, 70.

Macrocorax fusicapillus (Gray).

D. corvina[5] Fuhrmann, 1905. ? Fuhrmann, 1908, 46; 1911, 251.

PASSERIFORMES—*continued.*

Manucodia chalybeata Penn.

D. paradisea Fuhrmann, 1909.

Merula merula (L.).

D. spinosissima (v. Linstow, 1894, 336). Blanchard, 1899 *a*, 206 and 214.

Mino dumonti Less.

D. corvina[5] Fuhrmann, 1905. ? Fuhrmann, 1908, 46; 1911, 251.

Oriolus galbula (L.).

D. compacta Clerc, 1906. Neslobinsky, 1911, 436.

D. frontina (Dujardin, 1845). Stiles, 1896 *b*, 54.

Philemon citreigularis (Gould).

D. conopophilae Johnston, 1912, 111.

Rupicola rupicola (L.).

D. uniuterina Fuhrmann, 1909.

Sphecotheres maxillaris (Lath.).

D. sphecotheridis Johnston, 1914, 106.

PICIFORMES.

Celeus elegans (P. L. S. Müll.).

D. longispina Fuhrmann, 1909.

D. lutzi Parona, 1901. Fuhrmann, 1909, 112.

Ceophloeus lineatus (L.).

D. longispina Fuhrmann, 1909.

D. cruciata (Rudolphi, 1819).

Colaptes auratus.

D. rhynchota Ransom, 1909, 10.

D. comitata Ransom, 1909, 15.

Colaptes campestris (Vieill).

D. frontina (Dujardin, 1845).

Drendrocoptes medius (L.).

D. frontina (Dujardin, 1845). Neslobinsky, 1911, 436.

Drendrocopus major (L.).

D. frontina (Dujardin, 1845). Stiles, 1896 *b*, 54.

Gecinus canus (Gm.).

D. cruciata (Rudolphi, 1819).

Gecinus viridis (L.).

D. frontina (Dujardin, 1845).

[1] Synonym: *D. oligophora* Magalhães 1898.

[2] Synonyms: ? *Taenia agama* Mégnin; *T. cesticillus* var. *phasianorum* Neumann; ? *T. infundibuliformis* var. *phasianorum* Mégnin; *Davainea guevillensis* Mégnin.

[3] Not *D. globocaudata* Cohn 1901 as given by Fuhrmann, 1908.

[4] Synonyms: *Taenia calva* Baird, 1853; *T. microps* Diesing 1857; *T. tumens* Mehlis.

[5] Synonym: *D. polycalcarea* v. Linstow, 1906.

PICIFORMES—*continued.*

Melanerpes erythrocephalus (L.).
D. comitata Ransom, 1909, 15.
D. rhynchota Ransom, 1909, 10.

Picus martius L.
D. frontina (Dujardin, 1845). Neslobinsky, 1911, 436.

Picus sp.
D. cruciata (Rudolphi, 1819). Fuhrmann, 1908, 46; 1909, 111.
D. longispina Fuhrmann, 1909.
D. frontina (Dujardin, 1845).
D. lutzi Parona, 1901

PSITTACIFORMES.

Ara aureicollis Cass.
D. leptosoma (Diesing, 1850).

Ara macao (L.).
D. leptosoma (Diesing, 1850).

Ara maracana (Vieill.).
D. leptosoma (Diesing, 1850).

Ara macavuanna (Gm.).
D. leptosoma (Diesing, 1850).

Ara nobilis (L.).
D. leptosoma (Diesing, 1850).

Ara severa (L.).
D. leptosoma (Diesing, 1850).

Cacatua galerita (Lath.).
D. cacatuina Johnston, 1912, 109.

Cacatua roseicapilla Vieill.
D. leptosoma (Diesing).

Cacatua triton macrolopha (Rosenb.).
D. psittacea Fuhrmann, 1911, 255.

Chrysotis purpurea.
D. leptosoma (Diesing, 1850).

Conurus guaronba (Gm.).
D. leptosoma (Diesing, 1850).

Electus pectoralis aruensis (Gray).
D. microscolecina Fuhrmann, 1909. Fuhrmann, 1911, 254.
D. oligorchidna Fuhrmann, 1911, 256.

PSITTACIFORMES—*continued.*

Electus rosatus (Müll.).
D. microscolecina Fuhrmann, 1909. Fuhrmann, 1911, 254.

Lorius garrulus (L.).
D. macroscolecina Fuhrmann, 1909.

Pionopsittacus pileatus (Scop.).
D. macroscolecina Fuhrmann, 1909.

Pionus fuscus (Müll.).
D. leptosoma (Diesing, 1850).

Psittacus erythacus L.
D. crassula (Rudolphi, 1819). Clerc non Fuhrmann. Stiles, 1896 *b*, 53.
D. leptosoma[1] (Diesing, 1850.) Stiles, 1896 *b*, 54.

Psittacus sp.
D. macroscolecina Fuhrmann, 1909.

Trichoglossus cyanogrammus nigrogularis Gray.
D. aruensis Fuhrmann, 1911, 255.

PTEROCLIDIFORMES.

Pteroclidurus namaquus (Gm.).
D. leptotrachela Hungerbühler, 1910, 512.

RHEIFORMES.

Rhea americana L.
? *D. struthionis* (Parona, 1885).

STRUTHIONIFORMES.

Struthio australis Gurn.
D. linstowi Meggitt (present paper). Hungerbühler, 1910, 511.

Struthio camelus L.
D. struthionis (Parona, 1885).

Struthio masaicus Neu.
D. beddardi Meggitt (present paper).
D. struthionis (Parona, 1885). Beddard, 1915, 589.

Struthio molybdophanos Reichen.
D. linstowi Meggitt (present paper). Beddard, 1915, 589. Blanchard, 1899 *a*, 206. v. Linstow, 1893, 447.

Reptilia.

Lacerta muralis.
D. hertwigi Mola, 1907 *a*, 575, cysticercoid.

[1] Synonyms: *Taenia longissima* Goeze, *T. filiformis* Rudolphi.

Insecta.

Musca domestica L.
D. tetragona (Molin, 1858), cysticercoid. Ackert, 1919, 28. Guberlet, 1916 *a*, 233.

D. cesticillus Ackert, 1918, 41. Guberlet, 1916 *a*, 233.

Mollusca.

Limax agrestis L.
D. proglottina (Davaine, 1870), cysticercoid.

Limax variegatus Drap.
D. proglottina (Davaine, 1870), cysticercoid.

Limax cinereus Lister.
D. proglottina (Davaine, 1870), cysticercoid.

Hosts unknown.

D. appendiculata Fuhrmann, 1909.

D. echinata Fuhrmann, 1909.

Key to Species of Davainea.

	Genital pores unilateral, suckers armed	*Aa*
	Genital pores unilateral, suckers unarmed	*Ab*
	Genital pores alternate, suckers armed	*Ba*
	Genital pores alternate, suckers unarmed	*Bb*
	Aa.	
1.	Eggs singly in the parenchyma	(2)
	Eggs in groups in capsules	(13)
2.	Proglottides with lateral appendages	*D. appendiculata* Fuhr.
	Proglottides without lateral appendages	(3)
3.	Rostellum with accessory spines	(4)
	Rostellum without accessory spines	(5)
4.	Rostellar hooks in two rows	*D. sphecotheridis* John.
	Rostellar hooks in form of a rosette with eight limbs	*D. rhynchota* Rans.
5.	Testes 2	*D. contorta* Zsch.
	Testes more than two	(6)
+		
6.	Cirrus-sac nearly reaching aporal margin	(7)
	Cirrus-sac not passing centre of proglottis	(8)
7.	Rostellar hooks 400, 15μ long	*D. compacta* Clerc.
	Rostellar hooks 300, 6–7μ long	*D. sphaeroides* Clerc.
	Rostellar hooks 200, 14–16μ long	*D. cruciata* Rud.
	Rostellar hooks 160–180, 9–10μ long	*D. numida* Fuhr.
8.	Rostellar hooks 400	*D. compacta* Clerc.
	Rostellar hooks 200	(9)
	Rostellar hooks 120 or less	(10)
9.	Rostellar hooks 14–16μ long	*D. cruciata* Rud.
	Rostellar hooks 22–23μ long	*D. paradisea* Fuhr.
10.	Testes 100	(11)
	Testes 50 or less	(12)
11.	Rostellar hooks 12μ long	*D. retractilis* Stiles
	Rostellar hooks 22–23μ long	*D. paradisea* Fuhr.

KEY TO SPECIES OF DAVAINEA—*continued.*

12.	Rostellar hooks 90	*D. madagascariensis* Dav.
	Cirrus-sac not passing nerve-cord; rostellar hooks 80	*D. corvina* Fuhr.
	Cirrus-sac reaching lateral excretory vessel; rostellar hooks 120	*D. gracilis* Jan.
13.	Accessory hooks posterior to rostellum . . .	*D. frontina* Duj.
	Accessory hooks absent . . . . . (14)	
14.	Testes extending laterally beyond nerve. . .	*D. penelopina* Fuhr.
	Testes not extending laterally beyond nerve . . . . (15)	
++		
15.	Cirrus-sac not reaching excretory vessels . . . . (16)	
	Cirrus-sac reaching or passing excretory vessels . . . (24)	
	Cirrus-sac nearly reaching to aporal excretory vessels	*D. sphaeroïdes* Clerc.
+++++		
16.	Egg-capsules extending laterally beyond excretory vessels. (17)	
	Egg-capsules not extending laterally beyond excretory vessels . . . . . (20)	
++++		
17.	Egg-capsules containing 2–3 eggs . . . . . (18)	
	Egg-capsules containing more than 5 eggs . . . . (19)	
18.	Receptaculum seminis present	*D. friedbergi* v. Lins.
	Receptaculum seminis absent	*D. multicapsulata* Fuhr.
19.	Rostellar hooks 140, 5μ long	*D. cyrtus* Skr.
	Rostellar hooks 120, 10μ long	*D. ceylonica* Bacz.
	Rostellar hooks 100, 6–9μ long	*D. tetragona* (Molin)
+++		
20.	Three layers of longitudinal muscles . . .	*D. spiralis* Bacz.
	Two layers of longitudinal muscles . . . . . (21)	
21.	Testes 5–6	*D. oligorchidna* Fuhr.
	Testes more than 12 . . . . . (22)	
22.	Rostellar hooks 80	*D. comitata* Rans.
	Rostellar hooks more than 150. . . . . (23)	
23.	Egg-capsules contain 3–6 eggs	*D. galeritae* Skrj.
	Egg-capsules contain 6–12 eggs	*D. microscolecina* Fuhr.
	Egg-capsules contain 10–14 eggs	*D. psittacea* Fuhr.
	?	*D. werneri* Klap.
24.	20 eggs per egg-capsule . . . . . (25)	
	12 eggs or less per egg-capsule . . . . . (26)	
25.	Rostellar hooks 200, testes 20–30	*D. pintneri* Klap.
	Rostellar hooks 120, testes 35–40	*D. gracilis* Jan.
	Rostellar hooks 70, testes 60	*D. leptosoma* (Dies.).
26.	Testes 15 or less.	*D. trapezoides* Jan.
	Testes 20 or more . . . . . (27)	
27.	Rostellar hooks 8μ long	*D. crassula* (Rud.) Clerc.
	Rostellar hooks 10μ long, egg-capsules extending laterally to excretory vessels	*D. volzi* Fuhr.
	Rostellar hooks 10–13μ long, egg-capsules not extending laterally to excretory vessels . . .	*D. microscolecina* Fuhr

KEY TO SPECIES OF DAVAINEA—*continued.*

Rostellar hooks 14μ long, egg-capsules extending laterally to excretory vessels . . . . . *D. clavicirrosa* Fuhr.
? . . . . . *D. gracilis* Jan.

\+ *D. cantaniana* Polonio and *D. blanchardi* Parona here.
\++ *D. capillaris* Fuhr., *D. penetrans* Bacz. here.
\+++ *D. circumvallata* (Krabbe)—when young—and *D. echinobothrida* (Mégnin)—when with unilateral genital pores—here.
++++ *D. cohni* Bacz.
+++++ *D. insignis* Steud., *D. urogalli* (Modeer).

Ba.

1. Proglottides less than 10 . . . . . (2)
   Proglottides numerous . . . . . (5)
2. Testes 4 . . . . . *D. himantopodis* John.
   Testes 10 or more . . . . . (3)
3. Testes lateral or anterior . . . . . *D. varians* Sweet
   Testes in a double row along posterior margin of proglottis (4)
4. Rostellar hooks 60, 7–8μ long . . . . . *D. dubius* Meggitt
   Rostellar hooks 80–95, 5–7·5μ long . . . . *D. proglottina* (Dav.)
5. Cirrus-sac not reaching excretory vessel . . . . (6)
   Cirrus-sac reaching or passing excretory vessel . . . (8)
6. Egg-capsules contain one egg . . . . . *D. polycalceola* Jan.
   Egg-capsules contain several eggs . . . . . (7)
7. Female organs in poral half of proglottis . . *D. leptotrachela* Hung.
   Female organs in centre of proglottis . . . . . (7*a*)
7*a*. Testes 20–30 . . . . . *D. echinobothrida* (Még.).
   Testes 10–15 . . . . . *D. cohni* Bacz.
8. Rostellar hooks 8μ or less . . . . . (9)
   Rostellar hooks 11μ or more . . . . . (10)
9. Suckers armed with 3 rows of hooks . . . *D. hertwigi* Mola.
   Suckers armed with 6–8 rows of hooks . . . *D. pluriuncinata* Crety
10. Genital pore anterior, in birds . . . . . *D. retusa* Clerc.
    Genital pore anterior, in birds . . . . . *D. hertwigi* Mola.
    Genital pore posterior, in rodents . . . . *D. salmoni* Stiles

Ab.

1. Proglottides 5 . . . . . *D. paucisegmentata* Fuhr.
   Proglottides numerous . . . . . (2)
2. A wavy line of accessory hooks present . . . *D. echinata* Fuhr.
   Accessory hooks absent . . . . . (2*a*)
2*a*. Rostellar hooks thorn-shaped . . . . . *D. formosana* Akashi.
   Rostellar hooks T-shaped . . . . . (3)

\+
3. Eggs singly in parenchyma . . . . . (4)
   Egg-capsules contain several eggs . . . . . (5)
4. Rostellar hooks 14–16μ long . . . . . *D. longispina* Fuhr.
   Rostellar hooks 20–30μ long . . . . . *D. struthionis* (Par.)
   Rostellar hooks 25–28μ long . . . . . *D. undulata* Fuhr.

KEY TO SPECIES OF DAVAINEA—*continued.*

5.	Rostellar hooks 75–88μ long	(6)
	Rostellar hooks 25–28μ long	*D. undulata* Fuhr.
	Rostellar hooks less than 20μ long	(7)
++++		
6.	Cirrus-sac reaching excretory vessels . . .	*D. linstowi* Meggitt
	Cirrus-sac not reaching excretory vessels . .	*D. beddardi* Meggitt
7.	Testes forming a ring round the female organs .	*D. cryptacantha* Fuhr.
	Testes lateral and posterior to female organs. . . .	(8)
8.	Genital cloaca with powerful sphincter muscle .	*D. macrocirrosa* Fuhr.
	Sphincter muscle of genital cloaca weak or absent . .	(9)
++		
9.	Testes less than 15	(10)
	Testes more than 20	(11)
10.	Rostellar hooks 120, 9–10μ long	*D. paucitesticulata* Fuhr.
	Rostellar hooks 300, 14–16μ long	*D. calcarea* Fuhr.
	Rostellar hooks ?, 6–7μ long	*D. crypturi* Fuhr.
11.	Rostellar hooks 9μ long or less	(12)
	Rostellar hooks 12μ or more	(14)
12.	Egg-capsules extending laterally beyond excretory vessel.	*D. crypturi* Fuhr.
	Egg-capsules not extending laterally beyond excretory vessel	(13)
13.	Cirrus-sac reaching excretory vessel . . .	*D. goura* Fuhr.
	Cirrus-sac not reaching excretory vessel . .	*D. lateralis* Bourq.
14.	Rostellar hooks 500, 14μ long	*D. provincialis* v. Linstow
	Rostellar hooks 350 or less	(15)
+++		
15.	Egg-capsules contain 4–5 eggs	*D. lateralis* Bour.
	Egg-capsules contain 8 eggs or more	(16)
16.	Testes 20	(17)
	Testes 50 or more	(18)
17.	Rostellar hooks 180–200	*D. aruensis* Fuhr.
	Rostellar hooks 350	*D. macroscolecina* Fuhr.
18.	Genital pore anterior	*D. globirostris* Fuhr.
	Genital pore half-way.	*D. leptacantha* Fuhr.
	Genital pore posterior	*D. uniuterina* Fuhr.
+	*D. micracantha* Fuhr. here.	
++	*D. lutzi* Parona here.	
+++	*D. lutzi* Parona here.	
++++	*D. lateralis* Bourq., *D. macroscolecina* Fuhr. here.	

Bb.

1.	Rostellar hooks absent	(2)
	Rostellar hooks present	(3)
2.	Length 17 mm., genital pore ventral to proglottis margin	*D. voluta* (v. Linstow)
	Length 21 mm., genital pore marginal . . .	*D. parva* v. Jan.
3.	Rostellum longer than broad, 40 hooks, 27μ long .	*D. campanulata* Fuhr.
	Rostellum broader than long	(4)

KEY TO SPECIES OF DAVAINEA—*continued*

++		
4.	Eggs singly in parenchyma	(5)
	Egg-capsules contain several eggs	(12)
+		
5.	Rostellar hooks 34, 21–23μ long	*D. oligocantha* Fuhr.
	Rostellar hooks over 100, under 18μ long	(6)
6.	Testes less than 20	(7)
	Testes more than 20	(9)
7.	Rostellar hooks 14–16μ long	*D. anatina* Fuhr.
	Rostellar hooks 9μ long	(8)
8.	Length ·85 mm.	*D. minuta* Cohn
	Length 150–200 mm.	*D. magnicoronata* Fuhr.
9.	Rostellar hooks 7–11μ long, testes 20–30	(10)
	Rostellar hooks 16–18μ long, testes 40–50	(11)
10.	Cirrus-sac ·24 mm. long	*D. columbae* Fuhr.
	Cirrus-sac ·15 mm. long	*D. cesticillus* (Molin)
11.	Egg-capsules extend laterally beyond excretory vessels	*D. polyuterina* Fuhr.
	Egg-capsules not extending laterally beyond excretory vessels	*D. nana* Fuhr.
12.	Testes less than 20	(7)
	Testes more than 20	(13)
++		
13.	Rostellar hooks 70	*D. crassula* (Rud.) Fuhr.
	Rostellar hooks over 150	(14)
	Rostellar hooks 800	*D. circumvallata* (Krabbe)
14.	Rostellar hooks 27μ long	*D mutabilis* Rüth.
	Rostellar hooks 16μ long	(15)
15.	3–4 eggs per egg-capsule	*D. laticanalis* Skrj.
	8–12 eggs per egg-capsule	*D. elongata* Fuhr.

\+ *D. microcotyle* Skrj.

++ *D. spinosissima* v. Linstow.

(The literature of the following species not being accessible to me, they are not included in the above key: *D. proglottina* var. *dublanensis* Kowalewski, 1905; *D. cacatuina* Johnston, 1912; *D. conopophilae* Johnston, 1912; and *D. vagintivasus* Skrjabin, 1914.)

In addition, lack of adequate description prevents the following species from being included: *D. asiatica* von Linstow, 1901; *D. australis* (Krabbe, 1869); *D. brachyrhnycha* (Creplin, 1853); *D. celebensis* von Janicki, 1902; *D. circumcincta* (Krabbe, 1869); *D. difformis* (Rudolphi, 1819); *D. emperus* Skrjabin, 1914; *D. globocephala* Fuhrmann, 1909; *D. longicollis* (Molin, 1858); *D. macrocirrosa* Fuhrmann, 1909; *D.* sp. Parona, 1909; *D.* sp. Johnston, 1912; *D.* sp. Johnston, 1912; *D.* sp. Douthitt, 1916; *D.* sp. Vevers, 1920; *D.* sp. Vevers, 1920; *D.* sp. Meggitt (present paper).

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EXPLANATION OF PLATE I.

REFERENCE LETTERS.

c. Cirrus-sac. *e*. Egg. *l.m*. Inner longitudinal muscles. *l'.m'*. Outer longitudinal muscles. *ov*. Ovary. *r*. Rostellum. *r.r*. Rostellar ridge. *r.s*. Receptaculum seminis. *s*. Sucker. *t*. Testes. *t.m*. Transverse muscles. *u*. Uterus. *v*. Vagina. *v.exc* Ventral excretory vessel. *w*. Wall of egg-capsule. *w'*. Inner wall of egg-capsule.

PLATE I.

Fig. 1. *Cotugnia brotogerys* Meggitt. Scolex.
Figs. 2–4. *Davainea beddardi* n. sp.
Fig. 2. Scolex.
Fig. 3. Musculature of proglottis from centre of strobilus.
Fig. 4. Musculature of proglottis from anterior portion of strobilus.
Figs. 5–7. *Davainea* sp.
Fig. 5. Musculature of proglottis.
Fig. 6. Transverse section of egg-sac containing eggs.
Fig. 7. Proglottis with genital organs.

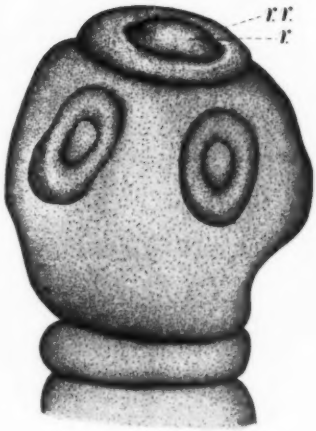

Fig. 1

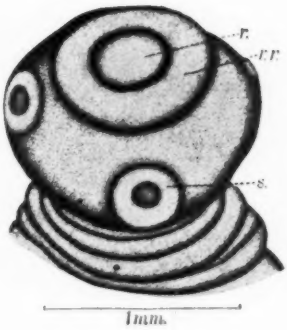

Fig. 2

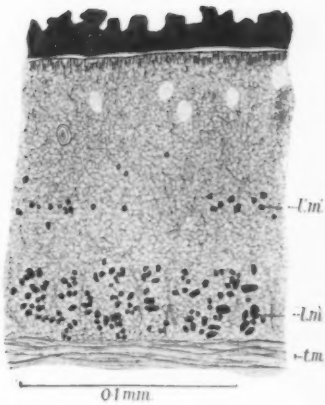

Fig. 3

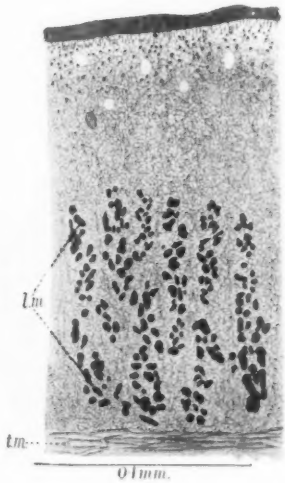

Fig 4

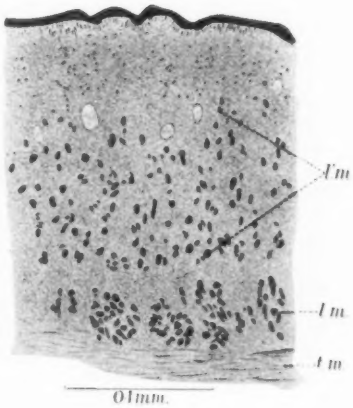

Fig. 5

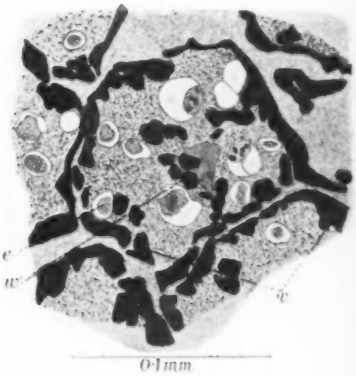

Fig. 6

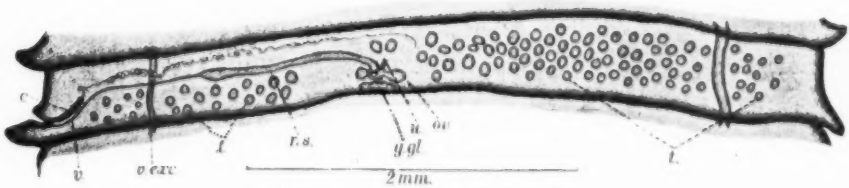

Fig. 7

A BACILLARY INFECTION OF THE COPULATORY APPARATUS OF *PEDICULUS HUMANUS*.

By J. A. ARKWRIGHT and A. BACOT.

(*From the Lister Institute of Preventive Medicine.*)

In the paper on the association of *Rickettsia* with Trench Fever, by Arkwright, Bacot and Duncan (1919) mention is made of a bacillary infection of the excreta and guts of lice (*Pediculus humanus*). A Gram-negative cocco-bacillus was isolated in pure culture. It was non-motile, fermented glucose, mannite and lactose very slowly, and formed acid and clot in milk in about 14 days.

It was not pathogenic for guinea-pigs. When plated from pure culture, rough and smooth colonies were formed similar to those which are known to occur in bacilli of the *B. coli* group.

Continuation of our work with *Pediculus humanus* has placed us in possession of further information concerning the relation of this bacillus to its host.

Sections of lice from a stock which has been inbred for nearly five years show a high percentage infested with this parasite. It is probable that crowding together in boxes for so long a period has caused these lice to be more uniformly infected than wild ones. In male lice the cocco-bacilli are seen in the folds of the *vesica penis*, whereas in females they occur in the vaginal orifice and passage leading to the ovaries[1]. No evidence that the gut is involved has been obtained from the very numerous sections examined.

Preliminary culture experiments with the guts of 24 lice taken at random from the stock were carried out. The insects were washed in 2 per cent. lysol followed by rinsing in sterile salt solution and the alimentary tract was dissected out on flamed slides with sterilised needles. Each specimen was transferred by means of a platinum loop to a separate nutrient agar tube and placed at the lower part of the slope.

Half the tubes were placed under anaerobic conditions, six at 35° C., and six at 26·5° C.; the remaining twelve were incubated aerobically at similar temperatures. Growth took place in seven of the twelve kept at the lower temperature, including both aerobic and anaerobic tubes. Subsequently five of the remaining tubes, which had been transferred to the cooler incubator, also produced growths. All the cultures appeared similar both to the naked eye and on microscopic examination. Subcultures were plated from the tubes and found to be pure. Both subcultures and plates were made with ordinary

[1] See Nuttall (1917), *Parasitology*, IX. 293 for description of copulatory apparatus of ♂ and ♀.

nutrient agar and were kept aerobically at 35° C. Later attempts to cultivate direct from the dissected guts at 35° C. have proved successful, so that the failures at this temperature in the first trial must be attributed to some chance circumstance. It may be noted here that to dissect out the alimentary system of the louse without contaminating it with organisms infesting the copulatory apparatus would be very difficult if not impossible, as the pressure of the dissecting needles would tend to release the valves which close the openings to both the male and female organs. The later series of trials was therefore planned in order to decide whether the gut was infected or not.

Six males, six females, and a like number of nymphs (in which the copulatory apparatus is not yet developed), were taken from the stock and treated in the same manner as in the previous experiment except that the two terminal segments were left adhering to the gut.

This experiment resulted as follows: six of the tubes containing the female and five of those containing the male guts produced growths of similar appearance to those in the previous experiment. Microscopically, when stained by Gram's method, they all showed similar cocco-bacilli, apparently in pure culture. Subcultures on plates from two tubes selected at random from among the eleven infected supported this assumption. As regards the tubes containing the dissections of the guts of nymphs only one showed a growth, and this was obviously contaminated as the growth started apart from the introduced gut, was of an entirely different appearance and was composed of Gram-positive bacteria.

Cultivation therefore strongly supports the microscopic evidence obtained from sections. We conclude that this bacterium may be correctly termed a parasite of the copulatory apparatus of *Pediculus humanus* and we propose for it the name of *Bacillus pediculi*.

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AN HEREDITARY *RICKETTSIA*-LIKE PARASITE OF THE BED BUG (*CIMEX LECTULARIUS*).

By J. A. ARKWRIGHT, E. E. ATKIN and A. BACOT.

(*From the Lister Institute of Preventive Medecine.*)

(With Plate II and 1 Text-figure.)

The Known Species of *Rickettsia*.

The forms under consideration resemble *Rickettsia prowazeki*—the supposed cause of typhus fever—which occurs in lice that have fed on typhus fever patients.

It may therefore not be amiss to describe briefly the organisms which have been grouped by various workers in the same category as *Rickettsia*.

The general characters of "Rickettsia" may be summarised as follows:

(*a*) Bodies of minute size, usually 0·5μ in diameter or less, of round or diplococcal shape, though very minute bacillary and even thread-like forms occur.

(*b*) Though resembling very small bacteria in general appearance, they stain much less readily than ordinary bacteria but can be coloured with Giemsa's stain; they are readily decolourised by Gram's method.

(*c*) Absence of motility.

(*d*) Resistance so far, with one exception, to attempts made to cultivate them on artificial media *in vitro*.

(*e*) Their occurrence in very large numbers in the gut and in some cases in other organs of blood-sucking insects.

The known organisms apparently belonging to this group are:

(1) The organism found in the tick—*Dermacentor venustus*—the invertebrate host of the parasite causing Rocky Mountain spotted fever.

This was first described by Ricketts and has since been very thoroughly studied by Wolbach (1919) and called by him *Dermacentroxenus rickettsi*.

It is found in very large numbers in the alimentary canal, salivary glands, muscles and other organs of the tick and is passed on to the next generation of ticks. Similar forms have been described in the blood of men and other animals infected with this disease; Wolbach records its regular occurrence in the tissues of the mammalian host. This organism varies considerably and according to Wolbach, has three distinct morphological forms.

(2) *R. prowazeki* described in detail by da Rocha-Lima (1916) and previously by Ricketts (1909) and Sergent, Foley and Vialatte (1914). This is found in

masses inside the cells of the mid-gut of *Pediculus humanus* after the latter has fed on typhus patients. Although often present in large numbers free in the gut, it appears to multiply inside the epithelial cells. Wolbach and Todd (1920) have described similar forms in the tissues of human sufferers from typhus. The organism varies considerably in shape and size; usually it is round, diplococcal or oval, but often resembles short bacilli; thread forms also occur.

(3) *R. quintana* or *wolhynica*, first described by Toepfer (1916) as the cause of trench fever, occurs in enormous numbers in the lumen of the gut of lice (*P. humanus*) which have fed on trench fever patients. It is more constantly rounded, oval or diplococcal than *R. prowazeki* and is not known to have occurred in thread forms. This species also stains a deeper purple by Giemsa's method. Most writers agree that the organism does not occur inside cells. It may be identical with *R. pediculi*.

(4) *R. pediculi*, first described by Munk and da Rocha-Lima (1917) as an occasional inhabitant of the gut of normal (uninfected) lice and subsequently said by them to be present in trench fever lice. They say that it is indistinguishable from *R. quintana*. It seems probable that the supposedly normal lice in which the parasite has been found had fed upon convalescents from trench fever whose disease had not been diagnosed.

(5) A species of *Rickettsia* found in lice which had fed on persons suffering from "war nephritis" was described by Toepfer (1917), who believed that he could distinguish it from *R. prowazeki* and *R. quintana* by its morphology. This has not been confirmed.

(6) A form of *Rickettsia* which Munk and da Rocha-Lima (*loc. cit.*) found occasionally in a few batches of lice which had either fed on normal persons or on trench fever patients. Munk and da Rocha-Lima stated that the organism was larger and stained more deeply than *R. prowazeki*, that it occurred not only in the lumen of the gut but also inside the cells lining the alimentary canal, in contrast to *R. pediculi* and *R. quintana*. These writers also stated that the organism damaged the cells of the gut and interfered with the powers of the insect to digest blood; they believe it to be a special parasite of the insect and not to be associated with human disease. If Munk and da Rocha-Lima are correct in this opinion their organism resembles the next species and that found in *A. lectularius*, which is described in this paper, so far as restriction to the invertebrate host is concerned.

(7) *R. melophagi*. This organism has been described by Noeller (1917), Sikora (1918), Jungmann (1918), and others, who say it is constantly present in the middle part of the stomach of *Melophagus ovinus* (the sheep "ked"), in large numbers in the older adults, in smaller numbers in young adults, and even occurs in pupae or in very young adults which have not yet sucked blood. The parasite is, they believe, hereditary in the "ked" and not derived from the sheep. The forms described are slightly larger than those of *R. pediculi* or *R. prowazeki*, round, oval or diplococcal in shape. Threads have not been

observed and this organism lies on the surface of the epithelial cells. It has been cultivated on blood agar by Noeller and Jungmann.

(8) *R. ctenocephali* was found by Sikora (*loc. cit.*) in 20 out of 100 cat fleas examined. It is said to be very like *R. quintana*.

(9) The last-named writer found similar forms in smears from the Malpighian tubes of a mouse flea.

RICKETTSIA IN *C. LECTULARIUS*.

Our knowledge of the form we are about to describe, which has hitherto apparently escaped attention, resulted from an attempt to infect bugs with the virus of trench fever by feeding them on patients suffering from this disease. Examinations of smears made from the guts of these insects showed in nearly every case thread-like "bacteria" with some admixture of shorter, rod-like forms (Plate II, fig. 2).

Stained with Giemsa's stain there appeared to be an outer sheath which took the eosin rather lightly while in the interior were granules or groups of granules which stained more deeply and of a purplish hue.

In some cases these smears also showed numbers of small deeply staining coccal or diplococcal bodies which, although slightly larger than *Rickettsia* found in gut and excreta smears of lice that had been fed on trench fever patients, were still sufficiently like them in size and general appearance to suggest that they might be the same species modified by development in the body of an unusual host. The fact that these bodies were not detected in any of the earlier smears from control bugs, although the thread-like forms above described were present, led to unsuccessful attempts to infect two volunteers with the emulsified guts of infected bugs in which the *Rickettsia*-like bodies were present. The examination of further control smears showed, however, that these minute bodies were also present in bugs that had fed only on normal men.

Suspicion of a relation between the rod and thread forms and these minute bodies arose owing to the occurrence of darkly stained granules in the rod and thread forms.

That these minute bodies frequently escaped our notice in smears which showed the long bacterial forms, is due partly to their small size, which makes it difficult to recognise them unless a considerable number are present in a single field; the same difficulty has been found in the case of the Rickettsia of trench fever. The fact that their distribution is often very localised is, however, the chief cause of difficulty in their detection. Whereas the bacillary forms are nearly always generally distributed in smaller or larger numbers in smears of well teased guts or Malpighian tubules, the minute forms, even when present in large numbers, are frequently only to be found in proximity to fragments of the gut or tubules. In some smears they were only seen where they chanced to be escaping from the ruptured end of the gut or a

tubule and no doubt the stage of the parasite in the infected cells affects the readiness with which it is found.

Motility.

A study of fresh wet preparations by either transmitted light or dark ground illumination failed to reveal any signs of motility.

Staining.

The most effective staining process tried is the slow method with weak Giemsa stain as generally employed for Rickettsia work, viz. 1 drop of stain to 1 c.c. of distilled water applied for 10–24 hours. All the forms are decolourised by Gram's method; the rod and thread forms are only faintly stained by the fuchsin counter stain. Strong fuchsin produces only a slight effect on the long forms and does not satisfactorily stain the minute coccal or diplococcal bodies. With Giemsa's stain the parasite does not react uniformly, the character of the tissues in its immediate vicinity apparently exercises an influence on the staining process. Where infected cells have been ruptured immediately prior to fixation or if the parasite is included in unbroken cells the long forms stain more intensely than when they are free. In the former situation the stained organism is purple, or if red, shows a gradation to the purple of the internal granules instead of an abrupt transition. It would appear that once the bacillary forms are removed from their natural habitat they rapidly undergo some change which causes them to stain badly.

Cultivation.

Attempts were made to cultivate the organism on artificial media. All the ordinary media were tried, aerobically and anaerobically, and in addition Dorset's egg medium, Noguchi's medium for spirochaetes, Krumwiede and Pratt's (1913) semi-solid medium which is successful in the cultivation of *B. fusiformis*, and the body juices of a lepidopterous pupa (*Hadena oleracea*), but in each case without a positive result.

In view of the remote possibility of the organism being a stage in the developmental cycle of a spirochaete, some mice were inoculated by scarification and subcutaneous injection with infected Malpighian tubes of the bug but no spirochaetes appeared in the blood.

Evidence of the hereditary character of the parasite.

In the absence of evidence that the parasite had any second host, theoretical considerations based on the feeding habits of *Cimex lectularius* suggested that the organism must be passed on through the egg. An examination of smears made from the alimentary system of newly hatched unfed bugs showed that the latter were infected. Eggs washed in 2 per cent. lysol for five minutes and then in sterile salt solution contained both rod and thread forms, the

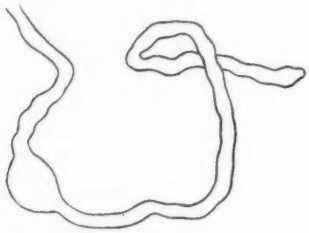
former being more common. This was also the case in smears of unhatched bugs extracted from the egg. Smears of eggs showing the early developmental stage of the bug (as a rule these eggs have to be dissected out of the ovary or made into smears soon after laying), contain immense numbers of more or less well-stained granules, usually poorly defined, but in some cases of distinct *Rickettsia* form and sharp in outline (Plate II, fig. 7); this feature may characterise the greater part of the smear. More frequently, however, it is confined to small patches in what are otherwise areas of ill-defined granules. Since we failed to cultivate the organism we cannot tell whether the ill-defined granules are related to the parasite or whether they are merely particles of protein. The sharply outlined forms are, we believe, undoubtedly a stage in the life-cycle of the organism. The minute bacillary forms that are present among the coccal and diplococcal forms are much more numerous in some smears than in others. Smears of the guts of embryo bugs at a late stage of development extracted from the egg, in some cases show masses of the minute forms deeply stained and clearly defined, lying within the lumen of the gut, where they have presumably been isolated as a part of the detritus of the embryonic process.

In order to obtain additional proof of hereditary infection, ovaries were dissected out of females that had been washed in lysol and then in sterile salt solution. Smears made from eggs extracted from these ovaries usually showed a few threads with some admixture of the shorter bacillary forms in addition to the granular infection alluded to above.

INTRACELLULAR MULTIPLICATION AND DEVELOPMENT.

Apart from its presence in the undifferentiated egg mass, the development of the parasite seems to be entirely intracellular. No evidence has been obtained of its multiplication in the lumen of the gut or in the body cavity where, however, thread forms have been found. Smears of teased embryos taken from developing eggs and of various organs from older bugs including the ovaries, testes, organ of Berlese and Malpighian tubes show minute coccal, diplococcal and lanceolate forms. These latter are slightly larger than the coccal and diplococcal (*Rickettsia*) forms and stain red instead of purple. Clusters of these red staining forms (Plate II, fig. 1), sometimes accompanied by a few of the *Rickettsia* forms, occur in the cytoplasm. They are best observed, individually, when the infected cell has been ruptured in such a manner as to spread its contents without breaking its nucleus. Very many examples of intermediate forms between these bodies and the longer bacterial forms have been observed; some clusters showed the lanceolate forms together with their various stages of growth into rods (Plate II, fig. 3). The intermediate forms were very often curved. Growth of the rods into threads is shown in almost every smear but apparently only in the enlarged cells of the Malpighian tubes do the threads attain their full length (Plate II, fig. 8).

The minute forms are also to be seen in some of the cells of teased guts in small numbers. In the cells of the seminal pocket on the ventral side of the fourth abdominal segment of adult females, known as the organ of Berlese[1], and in the cells of the Malpighian tubes clusters of the lanceolate forms are of frequent occurrence, sometimes very large ones (Plate II, fig. 4), while the *Rickettsia* forms are frequently present in immense numbers in the enlarged cells of the tubes in company with the thread forms. There would seem, however, to be a distinction between the course of intracellular development in the two organs in that, so far as present observation goes, threads and rods are comparatively scarce in the organ of Berlese, whereas they are exceedingly plentiful in the infected Malpighian tubes, generally in excess of the Rickettsia bodies. The longer bacterial forms are often present in the cells of certain portions of the gut wall, but they are never very numerous in any one cell.



Text-figure. Swelling in Malpighian tube of *Cimex lectularius* due to infection by the parasite. Camera lucida drawing from unmounted dissection of adult female.

Within the cells of the Malpighian tubes the multiplication of the parasites becomes so great that individual cells are swollen to more than twice their normal diameter. This has only been observed in the larger nymphs or adult bugs. It is not uncommon to see two or more tubes each with one or more swellings in the same insect and as the tubes at these points may be two or even three times their normal diameter (Text-figure) the infection is quite apparent under the dissecting microscope.

The enlarged cells in fresh preparations are more transparent than normal ones, sometimes showing a faint greenish hue in the centre of the swelling, and when opened they are found to be packed with the thread forms and granules in varying proportions (Plate II, fig. 8). In sections such cells have a bird's nest appearance owing to the intertwining of the long bacterial

[1] The process of fertilization in the bed bug differs very remarkably from that usual among insects. The penis is inserted into an opening in the right side of the ventral plate of the fourth abdominal segment of the female. Immediately above this opening lies a spherical organ consisting of a mass of cells known as the organ of Berlese. This organ has no duct or outlet and the spermatozoa penetrate through the mass of cells composing the organ into the body cavity, finding their way to the oviducts and fertilizing the eggs *in situ*. The development of the embryo is frequently well advanced before the egg is laid. (For further details see Craig (1915), *Indian Journal of Medical Research*, II. No. 3, pp. 698–705.)

forms (Plate II, fig. 6). Presumably such cells eventually rupture and discharge their contents into either the body cavity or the lumen of the tubule, but this process is not shown in any section yet examined.

RELATION OF THE *RICKETTSIA* BODIES TO THE THREAD FORMS.

Under dark ground illumination the thread forms have been observed to evacuate granules which, judging by their size, are similar to the darkly stained bodies seen within the thread forms in smear preparations.

Circumstantial evidence suggests that these granules are the same as the Rickettsia bodies which in the first instance attracted our attention and that in bugs which have fed these bodies are largely derived from disruption of thread forms.

PROBLEM OF THE INFECTION OF THE EGGS.

In addition to their development in certain cells of the alimentary system, thread forms have been found in the blood of the bug taken with a fine capillary pipette from the cut stump of one of the legs of a female and heavy infection of certain cells of the organ of Berlese has been observed in an apparently virgin female (no spermatozoa were observed either in this organ or in a smear of the ovaries which contained no developed eggs). The smear of the ovaries of this female also showed infection, but it was uncertain whether the egg cells were themselves infected. In the case of this apparently virgin female the form found in the sexual organs was chiefly the lanceolate form.

The testes of the males are also infected in some cases but no signs of the parasite were found in smears of the accessory glands of the same insects. As already stated there is no evidence that the organism is motile. It seems possible that the eggs may be infected by the spermatozoa but attempts to obtain evidence from teased preparations that the spermatozoa were infected gave only negative results.

GENERAL CHARACTER OF THE INFECTION.

Heavy infection with this parasite must be very general, if not universal, among bed bugs. The stock of bugs in which the parasite was first noticed originated from a few specimens taken from an old Essex cottage and as the insects had been confined in a small box and inbred for many generations prior to their use for the trench fever experiments above-mentioned, it is not surprising that almost every bug examined showed one or other of the forms of the parasite. Another race was obtained from an old house situated in Paddington and smears were made from bugs of this stock before breeding from it. Insects of this stock were also found to be generally infected. A further supply was obtained from animal cages in a London laboratory and examined without giving them any chance of further feeding, 19 out of 20 showing the presence of the parasite.

Bugs from two different sources in Warsaw were examined within a day or two of capture and all these were found to be infected.

Developmental cycle of the parasite.

The scheme set out below is merely tentative, all that is claimed for it is that it is a reasonable explanation of the observed facts and the excuse is offered that by linking up these facts a clearer picture can be conveyed than by the mere recital of the detached details. In the absence of any success in cultivation apart from the host, it is of course only possible to assume a connection between some of the forms in the order in which they are stated.

Starting with the eggs within the ovary, it seems most probable (*a*) that they become infected at the time of fertilisation with the *Rickettsia* form (Plate II, fig. 7), (*b*) that simple multiplication is followed by some of the first generation developing through a bacillary stage into threads while others continue simple multiplication *pari passu* with the presentation of suitable conditions due to the development of the embryo, (*c*) that owing to the massive granule infection of the egg material at this stage, cells of practically every organ of the growing embryo tend to become involved, but only in a certain number are the conditions necessary for intracellular multiplication afforded. In these, clusters of the minute *Rickettsia* forms develop, rapidly changing in favourable situations into the red-staining lanceolate forms through the development of an outer covering or envelope. These enlarge in due course into the long bacillary forms which in their turn release the darkly staining minute *Rickettsia* bodies. The large cells of the Malpighian tubules and their free unencumbered position allow of a much more massive infection than other situations; it is also possible that they afford more stable conditions during the moulting periods and bring the organisms into close proximity to the sexual glands when these are developed, thus increasing the chances of the latter becoming infected. In the course of the very numerous dissections which it has been necessary to make in the progress of this work, it has been noticed how frequently the enlarged cells occur in the distal third of the tubules.

Suggested name for the parasite.

The organisms known as *Rickettsia* are at present very incompletely described and only recognisable by their more superficial characters, such as morphology and localisation.

On such evidence it is not possible to decide with any certainty how near or remote the phylogenetic relationship of the members of the group to one another may really be, and the present writers therefore consider that Rickettsia should not be accepted as a generic name in the strict sense of the term to cover all the organisms referred to in their opening paragraphs. The smaller group comprising only those concerned with the three mammalian (human) diseases typhus, trench, and Rocky Mountain spotted fevers, would seem to form a more convenient unit.

Nevertheless, since the Rocky Mountain spotted fever organism has been

put into a new genus by Wolbach and on the other hand the form in the sheep "ked" which is not believed, however, to infect the sheep has been called *Rickettsia melophagi* it will be useful to retain *Rickettsia* as a group name for all in the present state of our knowledge. It is in this latter sense that we use it in tentatively naming the above-described parasite of the bed-bug *Rickettsia lectularia*.

Postscript.

A recent examination of the few specimens of *Cimex hirundinis* which comprise all the bugs of the genus *Cimex*, apart from *C. lectularius* we have been able to obtain up to the present, shows that this species is also parasitised in some of the same organs which are infected in *C. lectularius*. As both the ovaries and testes are involved it is very probable that this will also prove to be an hereditary infection. The organism is, however, much more bacillary in appearance, considerably larger in size and has different staining reactions; in spite of several similarities it is not possible in the present limited state of our knowledge to decide how nearly, if at all, it may be related to the organism described above. We hope to obtain further material to continue our research and should any of our readers be able to obtain living specimens of any of the species within the genus *Cimex*, other than *lectularius*, we shall be very grateful to them if they will send us some.

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DESCRIPTION OF PLATE II.

Fig. 1. Minute lanceolate forms issuing from ruptured cell of Malpighian tube (× 1000).
Fig. 2. Bacterial forms in fragment of gut wall (× 1300).
Fig. 3. A large cluster of lanceolate forms and developing bacterial forms issuing from ruptured cells of ovary (× 1000).
Fig. 4. Minute lanceolate forms issuing from ruptured cell of organ of Berlese (× 1300).
Fig. 5. Thread forms issuing from ruptured end of Malpighian tube (× 1000).
Fig. 6. Section through Malpighian tube showing mass of thread forms in infected cell (× 1000).
Fig. 7. Rickettsia and bacillary forms from smears of two eggs. The Rickettsia forms are more heavily stained than is usual in smears of eggs (× 1300).
Fig. 8. Smear of Malpighian tube showing Rickettsia and thread forms (× 1300).
Fig. 9. A range of forms selected from smears of various organs (× 1300).

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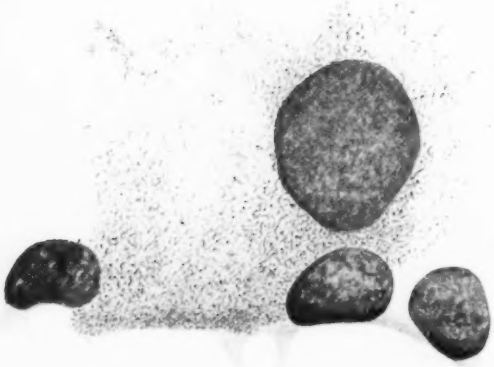

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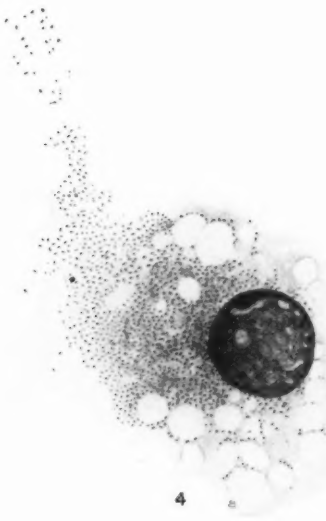

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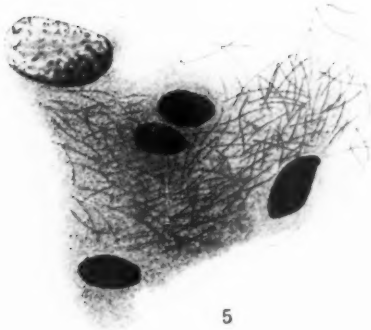

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ON THE LIFE HISTORY OF *ASCARIS LUMBRICOIDES*, L. PART V.

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(*From the Lister Institute of Preventive Medicine, London, and the Quick Laboratory, Cambridge.*)

(With 8 Text-figs.)

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I. Summary of the literature on the subject published during 1919 and 1920.

Since the publication of Part IV (Stewart, 1919), four papers dealing with the life-history of *Ascaris lumbricoides* have appeared.

(1) Ransom and Foster (1920) give a full account of their work, preliminary reports of which have already been published (1917 and 1919).

As evidence in the problem of whether the worm can undergo full development in one host alone, they attach great importance to two experiments, one on a kid and one on a lamb, in which after the administration of ripe eggs of *A. suilla*, they recovered worms from the intestines. In the kid, which died 24 days after the first feeding, the worms measured from 4·3 to 11·4 mm.; in the lamb, which was killed 103 days after feeding, the worms measured from 60 to 110 mm. The authors consider that, as *Ascaris* infection is uncommon in goats and sheep, the worms may without doubt be ascribed to the experimental feeding. They record five experiments on pigs which gave doubtful results, since the pigs fed with *Ascaris* eggs were found, after varying periods,

to be on the average less infected with *Ascaris* than pigs which were kept as controls, and had not been so fed.

They summarise their results as follows: "Stewart's observations as to the migration of *Ascaris* larvae through the lungs have been confirmed, but his suggestion that rats and mice act as intermediate hosts is not tenable. No intermediate host is necessary, and human beings and pigs become infected with *Ascaris* as a result of swallowing the eggs of the parasite, and not as the result of swallowing food, water or other substances that have been contaminated by the faeces of rats and mice." They base this view on the experiments referred to, and on the apparent death of larvae passed in the faeces of mice.

[I wish to emphasize that this view rests on the discovery which I was the first to make and to publish (Stewart, 1917 *a*), namely, that the larval development of the worm can take place in pigs as well as in rodents. Since making this observation I have asserted the possibility of direct infection. I maintained, however, that the mode of infection had not yet been conclusively demonstrated, that it was possible that the larvae passed in the faeces of mice were not actually dead, but in a condition of suspended animation, and that consequently indirect infection might also be possible.]

Ransom and Foster's paper is a very scholarly exposition of all work bearing on the subject. It contains sections on the relation of age to infestation which also exhibits the high frequency of the parasite among swine in the United States, on the egg stages of *Ascaris*, and on the life-history of related Nematodes. Of great theoretical interest is the observation that the larvae of *Ascaris anoura* apparently pass through the lungs of its host—a python—and reach a much higher stage of development there than do the larvae of *A. suilla* in the lungs of the pig.

In experiments on guinea-pigs the authors found *Ascarid* larvae in the lungs after the subcutaneous injection of ripe eggs of *A. suilla*. In feeding experiments they also found a small number of larvae in a few cases in the spleen and thyroid gland and under the peritoneum. They suggest the explanation that some young larvae may pass in the blood stream direct through the liver and lung, and thus entering the arterial system may be carried to situations remote from their normal route.

(2) Sadao Yoshida (1919) finds that hatching and larval migration of *A. lumbricoides* take place in guinea-pigs, monkeys and rabbits, and that human beings can be infected by larvae from the lungs of guinea-pigs. He has not yet completed the morphological study of the larvae.

(3) In a second paper, Yoshida (1919 *a*) develops the thesis that the larvae migrate through the serous sacs and direct through the tissues, not along the blood stream. This view he bases (1) on experiments in which he injected larvae extracted from the organs of one animal into the serous sacs of a second, and thereafter recovered them from remote tissues of the second animal. (2) In another series of experiments he administered ripe eggs by

the mouth, and found larvae not only in the liver and lungs, but in the abdominal cavity, spleen, pancreas, kidney, and pleural sacs.

He found larvae in the tissues at very short periods after infection, in one experiment in the pleura, lungs, abdominal cavity, liver, spleen, pancreas, and kidney after 20 hours only.

(4) I (Stewart, 1920) published a short summary of past work, and of some of the facts of distribution, and of the clinical importance of the parasite.

II. THE AUTHOR'S EXPERIMENTS DURING 1920.

The experiments dealt with in the present paper were conducted in the Lister Institute of Preventive Medicine during the summer of 1920, the cost of the animals used being borne by a grant from the Medical Research Council. The specimens secured were examined partly at the Lister Institute and partly at the Quick Laboratory, Cambridge. My thanks are due to the governing body of the Lister Institute, to the Medical Research Council, to Dr C. J. Martin and Dr MacConkey for much assistance, to Prof. Nuttall for his kind permission to work in the Quick Laboratory and for his help, and to Messrs C. and T. Harris of Calne for the supply of material.

The objects of the experiments were: (A) To ascertain whether after the administration of ripe eggs of *A. suilla* to pigs, the resulting worms could live and develop in the intestine after the 14th day. The experiments described in Part IV (Stewart, 1919), had traced the life-history to the 14th day, but I had failed to recover worms on the 19th day. (B) To observe whether larvae of *A. suilla*, passed in the faeces of mice, could infect pigs.

(A) *Experiments in which eggs of* A. suilla *were administered to four pigs.*

11. vi. 20. Ripe eggs of *A. suilla* from cultures 30–45 days' old, were given to four sucking pigs aged three days. Each pig received 20,000 to 30,000 eggs.

18. vi. 20. On the 7th day after infection all four pigs were seriously ill with pneumonic symptoms. Pig I died during the night, and larvae of *A. suilla* were found in enormous numbers in its trachea.

26. vi. 20. On the 15th day after infection Pig II was killed. *A. suilla* larvae, 3–5 mm. in length, were found throughout the small intestine, on the average one specimen in every centimetre of gut examined. The mucosa was in a catarrhal condition. Caecum and rectum negative.

28. vi. 20. On the 17th day after infection, Pig III was killed. *A. suilla* larvae, 4–7 mm. long, were found in its small intestine, one specimen in every 7 cm. of gut examined.

30. vi. 20. On the 19th day after infection, Pig IV was killed. *A. suilla* larvae, 6–7 mm. long, were found in its small intestine, one specimen in every 8 cm. of gut examined.

The foregoing experiments therefore resulted in the finding of larvae in the small intestine on the 15th, 17th and 19th days after infection. They had grown from 3 mm. on the 14th day to 7 mm. on the 19th.

(B) *Experiment in which* A. suilla *larvae in the faeces of mice were administered to two pigs.*

Ripe eggs of *A. suilla* were administered to eight mice. The faeces dropped by the mice on the 12th and 13th days after infection were collected, and found to contain immobile *Ascaris* larvae. After an interval of 14 days the faeces were administered to two sucking pigs three days old. The pigs were killed three days thereafter, and no worms were found in their intestines.

The experiment was therefore negative, but taking the technical difficulties into consideration, it would require to be repeated several times to establish with certainty that the larvae passed in the faeces of mice are non-infective.

III. The anatomy of the larvae of *A. Suilla* Duj. found on the 19th day after hatching in the small intestine of the pig.

Size. Length while alive 7 mm., when fixed in 70 per cent. alcohol 6·5 mm. Maximum breadth in alcohol 0·15 mm. *Head* (Fig. 1). 0·04 mm. long, lips connected at their bases by membrane, papillae as in the adult, no teeth, head separated from the body by a shallow circular groove. *Body.* Surface markings (1) annuli as in the adult, 0·005 mm. broad, (2) longitudinal ridges (Fig. 3) 30 to 32 in each (dorsal and ventral) half, ridges not continuous from one annulus to another nor in the same longitudinal line in successive annuli. Anus situate 0·2 mm. from the tip of the tail. *Tail.* As in the larva of the 14th day after hatching. *Cuticle* (Fig. 2). Consists of three layers, the mid-layer stains deeply with iron haematoxylin.

Lateral membranes (Figs. 2 and 4) extend from the neck nearly to the tip of the tail, are formed of all three layers of the cuticle, the mid-layer gives rise to the tri-radiate skeleton, the inner layer covers the lateral line and partly fills the triangular space underlying the skeleton with irregular lamellae. *Lateral lines* (Fig. 3) divided as in the adult by two very fine horizontal septa. The lateral canals are attached to their inner surfaces—*vide infra.*

Alimentary Canal. Mouth triangular in transverse section, funnel-shaped. Oesophagus 0·7 mm. long, simple club-shaped, slightly expanded also at anterior extremity; cuticular lining and outer membrane very fine; radial muscles well developed, embedded in a stroma of protoplasm, oval nuclei present in this stroma, number in front of nerve ring—in dorsal segment 5, in subventral segments 4 each; behind nerve ring—in dorsal segment 5, in left subventral 4, in right subventral 5; the posterior end of the dorsal segment contains the body of a large nucleus, which extends across the entire segment, and sends two branches forward along the upper edges of the subdorsal radii, and two branches downward and forward into the subventral segments.

Nerve ring. 0·182 mm. from the anterior extremity, contains one nucleus opposite each lateral line and each subventral muscle field.

Excretory system. Pore 0·238 mm. from the anterior extremity opposite the junction of the anterior and middle thirds of the oesophagus. The excretory duct is formed by the cells of the ventral line, and is lined by a fine membrane. The body of the excretory cell (Fig. 4) lies as usual beneath the oesophagus, joining the two lateral lines. The single large nucleus, 0·024 mm. long, lies in the left half of the cell. From the body two thin thread-like prolongations extend backward nearly to the level of the anus, intimately attached to the inner surfaces of the lateral lines (Fig. 3). Each prolongation contains a fine canal from its hind end to 0·5 mm. from its anterior extremity. It will thus be seen that these canals cannot be traced into the body of the cell or into connection with the excretory duct. The prolongations are the lateral canals.

Gonads. Male—a single solid rod of cells ventral to the intestine, 2 mm. long, extending forward from the anus. Female—vulva patent, in the ventral line, 3 mm. from the tip of the tail. The vagina extends backwards and slightly to the left, and divides into two utero-ovarian tubes, one lying ventral to the intestine, the other along its left side. The former reaches to 2 mm., the latter to 2·3 mm. from the tip of the tail.

IV. THE DEVELOPMENT OF CERTAIN ORGANS IN *A. SUILLA* DUJ. FROM THE EMBRYO AT HATCHING TO THE LARVA DESCRIBED IN SECTION III.

Cuticle and lateral membranes (Figs. 5, 6 and 7). In the embryo the cuticle is excessively fine, lateral membranes absent. The lateral membranes appear on the 5th day, and are recognisable both in larvae from the liver and from the lung: they are extremely small. They become more prominent, and the skeleton appears, during the passage up the bronchi and trachea on the 8th, 9th, and 10th days. The cuticle thickens markedly on the arrival of the larvae in the alimentary canal. The growth of the cuticle and lateral membranes appears to be continuous, and I have not observed any sign of an ecdysis[1].

Oesophagus. In the embryo it is represented by nuclei arranged as a narrow cylinder expanding at the hind end into a bulb. There is therefore no doubt as to the multicellular origin of the organ.

Excretory cell. The nucleus can be identified (Fig. 8) in the embryo on the left side, opposite the anterior end of the bulb. In sections of larvae of the fourth day after hatching, the cell can be seen to belong to the left lateral line. By the fifth day it has grown underneath the oesophagus across the mid-line, and established contact with the right lateral line. The lateral canals are formed between the 14th and 19th days after hatching. The excretory system, with the exception of the terminal portion of the duct, is composed of one very large branching cell only. The wall of the terminal portion of the duct is formed by cells of the ventral line.

[1] This statement refers only to larvae after entry into the tissues of the host. An ecdysis occurs immediately after hatching, in the alimentary canal of the host.

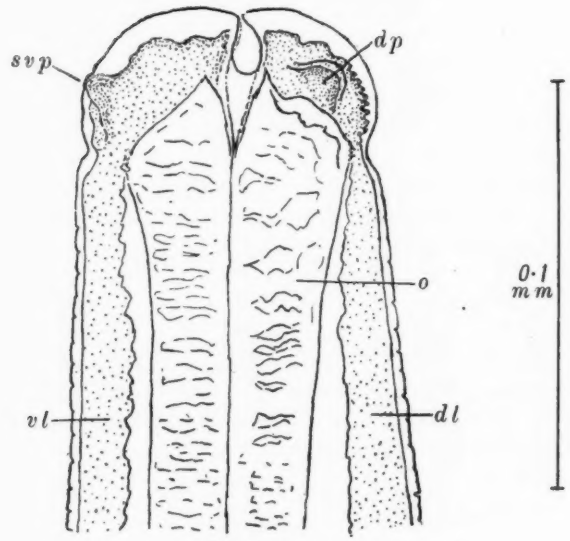


Fig. 1

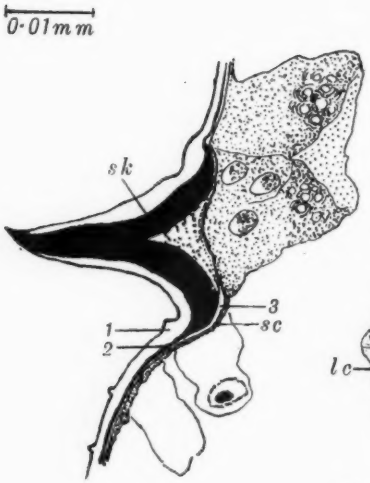


Fig. 2

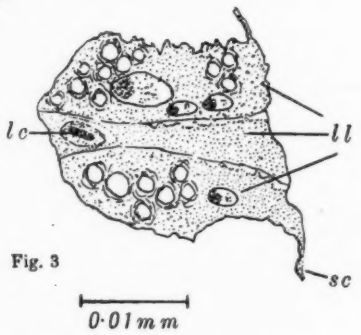
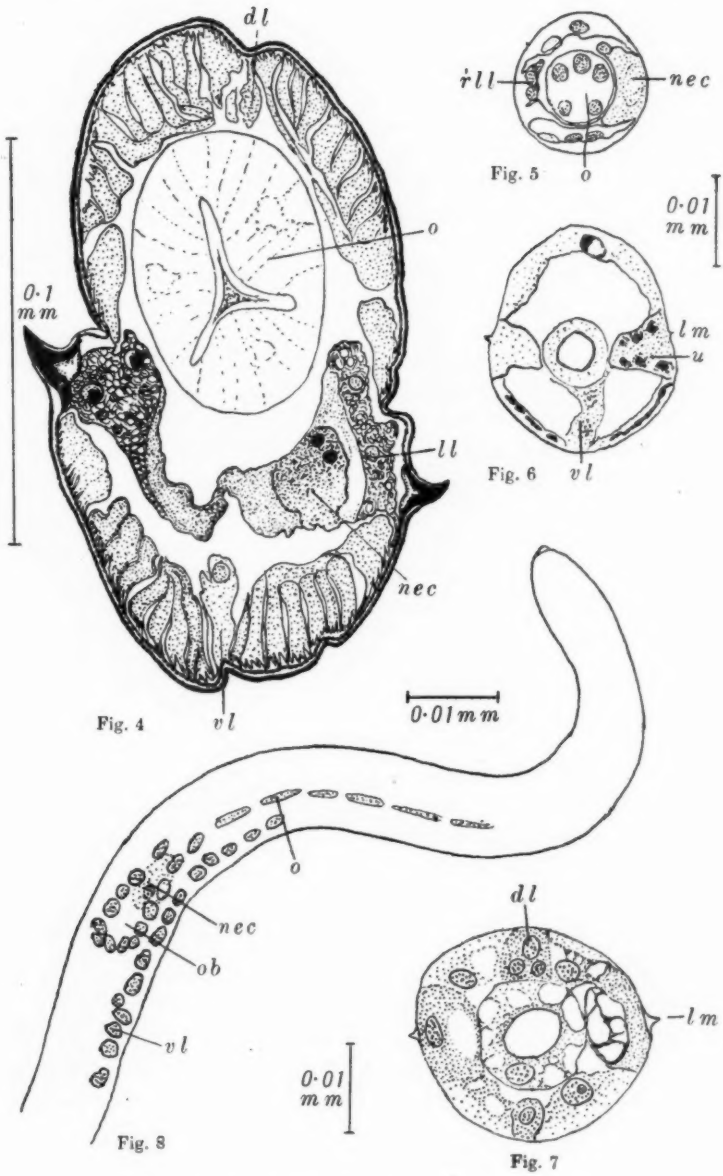


Fig. 3

Figs. 1–3. *Ascaris suilla* Dujardin. (See Legends, p. 47.)



Figs. 4–8. *Ascaris suilla* Dujardin. (See Legends, p. 47.)

V. The route taken by the larvae of *A. Suilla* Duj. in their migration through the tissues of the host.

The larvae of *Ascaris lumbricoides* and its relations live actually within the tissues of their hosts from the moment they perforate the walls of the intestine (assuming they do not ascend the bile ducts) until they reach the alveolar spaces of the lungs. Theoretically considered they could travel from the intestine to the lung along two paths, namely (1) by the veins and pulmonary artery, and (2) by the lymphatics and blood-vessels, and (3) by a third method directly through all intervening tissues, availing themselves only incidentally of such natural spaces as they encountered on the line which they happened to take.

The first is that which I suggested (Stewart, 1917, p. 226). It has been accepted with reservations by Ransom and Foster. It is the route followed by a minority of the larvae of *Agchylostoma*. The second is that followed by the majority of the Ankylostome larvae. Larvae coming from the small intestine would by this route traverse the lacteals, cysterna chyli, and thoracic duct to the left subclavian vein. The third route has been suggested recently by Yoshida. "It is believed that the larvae migrate in every direction boring through various organs or tissues by means of their own power of piercing but not by way of blood-vessels." "The general and important course of migration by the ascarid larvae in the body of the host may be as follows: The ascarid larvae proceed to the abdominal cavity by boring through the wall of the intestine. Thence they pierce the diaphragm to enter the pleural cavity, finally penetrating into the lungs from their surface. It might be considered as an additional and mere accidental course of migration that the larvae in the abdominal cavity penetrate into the liver, thence they are carried to the lungs by the way of blood-vessels, passing through the heart."

Yoshida advances the following arguments in favour of his hypothesis. (1) That he has found larvae in the abdominal cavity in large numbers during the first 48 hours, in lesser numbers thereafter. He has also found them in the pleural cavities and in organs lying off the direct blood route, viz. spleen, kidney, and pancreas. He also states that histological study shows "that almost all the larvae in the lungs and liver are not found in the blood vessels, but in other tissues." His infection experiments prove that the larvae can migrate from the serous cavities to the lungs.

The following considerations are opposed to this view: (1) In Yoshida's own experiments the liver was apparently found to contain as many larvae as the abdominal cavity during the first 48 hours. I have examined the pleural and abdominal cavities during the first 48 hours in three cases only, which of course do not permit of a conclusion, especially in view of Yoshida's very definite results, but I have failed to find larvae in these cavities, although they were present in the liver. (2) My experience of serial sections differs entirely from that of Yoshida. I have found that the majority of larvae in the

liver lie obviously in dilated blood capillaries, venules, and veins. In the latter situations they are surrounded on all sides by red blood corpuscles.

Ransom and Foster in one experiment found larvae in blood taken with a syringe from the portal vein, in another experiment one larva in blood from the pulmonary artery. They state, however, that accidental access of larvae from other sources could not be entirely excluded.

The following table shows the breadth of *Ascaris*, *Agchylostoma* and *Filaria* larvae, compared with the diameter of blood capillaries:

	Maximum breadth mm.
1. *Ascaris suilla* recently hatched, alive in salt solution ...	0·013
2. *Ascaris suilla* recently hatched, mounted in Canada balsam	0·0098
3. *Ascaris* larva of fifth day, from lung of rat, in weak sublimate solution	0·025
4. *Ascaris* larva of sixth day, from liver, in salt solution ...	0·034
5. *Agchylostoma duodenale* mature larva, living (Looss) ...	0·017
6. *Filaria bankrofti* larva from human blood, living (Manson)	0·008–0·011
7. Human capillary normally full of blood (Schäfer)	0·007–0·008

Comparing 1, 6 and 7, it is clear that an *Ascaris* larva within the first 24–48 hours could pass through a capillary with a moderate degree of dilatation, but that it would probably be delayed in the passage. Larvae of the fifth or sixth days would be much delayed, and might rupture the capillary.

The early appearance of larvae in the lungs, and in small numbers in remote organs such as the spleen and kidney, could be explained, as suggested by Ransom and Foster, by their passage direct in the blood stream through the liver, heart, and lungs. It is also possible that some traverse the lacteals, cysterna chyli, thoracic duct, subclavian veins, heart, and pulmonary artery, and thus reach the lungs without passing through the liver.

The marked degeneration and disintegration of the liver cells around the larvae would permit of slow abnormal dilatation of the capillaries by the older animals, and their passage onward into the hepatic venules and veins. Even if rupture of the capillaries occurs, the larvae regain the blood stream in the veins, as is seen in the sections referred to above.

Taking into consideration therefore the great frequency of the larvae in the liver, and their demonstrable presence in the blood vessels of this organ, I consider that the route described by me (Stewart, 1917, p. 226) is that followed by the great majority of the larvae, although a small proportion may doubtless follow the lymph stream, or perforate the diaphragm as described by Yoshida. In the blood and lymph streams they are guided by thigmotropism. It is not so easy to define the stimulus which would guide them under Yoshida's hypothesis, although we cannot believe that their movements are entirely anarchic.

VI. Mechanism of protection of the body against the invasion of *Ascaris* larvae.

Yoshida reports that larvae found in the pleural cavities are surrounded by groups of white blood corpuscles and histiocytes (Yoshida, 1919 *a*, p. 23). This is clearly the same phenomenon as the capture of the Ankylostome larvae in the lymph glands, two days after infection, as observed by Looss (1911, p. 521). This author showed that such larvae were killed by the lymphatic cells, and that this process forms part of the mechanism of defence. Strong infection stimulates the glands. "It seems as though the larvae were able to withstand the attacks of the lymphatic cells for a certain length of time or possibly also the lymphatic cells do not at once commence their attacks. If the larvae succeed in escaping from the glands within this time they are saved, if they do not succeed they fall a prey to the lymphatic cells." Captured larvae were observed in considerable numbers as early as two days after infection. In Yoshida's cases, the reaction occurred as early as 20 hours after feeding.

VII. The extent of natural *Ascaris* infestation of pigs in England and treatment suggested with a view to the eradication of the disease.

Messrs C. and T. Harris & Co. of Calne, Wiltshire, at my request, very kindly undertook the enumeration of pigs found to contain *Ascaris* in their abattoirs. Out of 370 stores, 62 or 16·75 per cent. contained this worm, out of 29 sows, 3 or 10·34 per cent. were affected. These figures are very low compared with the American returns of Raffensperger, who found 41·1 per cent. affected (Ransom and Foster, 1920, p. 25). To estimate the economic effect of the parasite in this country, further statistics of infection from all districts are required, and also extensive observations on the relative weight of infected and uninfected pigs. The facts given by myself (Stewart, 1918*a*, p. 203), although based on only 83 examinations, suggest the possibility of considerable loss from this cause.

Treatment. Since animals of two months and over appear to be only slightly susceptible to infection, it should be possible to free a herd completely of the parasite by a routine administration of santonin or oil of chenopodium, to all pigs at the ages of one and two months. Whether the adoption of such a routine on a large scale should be recommended or not, would depend on the results of the investigation suggested above.

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LEGENDS TO TEXT-FIGURES.

Figs. 1–8. *Ascaris suilla* Dujardin.

Fig. 1. Larva 19 days after hatching, from the intestine of the pig. Head.

Fig. 2. Larva 19 days after hatching. Transverse section through the lateral line and lateral membrane, 0·68 mm. from the anterior extremity.

Fig. 3. Larva 19 days after hatching. Transverse section through the lateral line, 1·1 mm. from the anterior extremity.

Fig. 4. Larva 19 days after hatching, from the intestine of the pig. Transverse section 0·35 mm. from the anterior extremity.

Fig. 5. Larva 4 days after hatching, from the liver of the mouse. Transverse section through the oesophageal region.

Fig. 6. Larva 5 days after hatching, from the liver of the rat. Transverse section through the intestinal region.

Fig. 7. Larva 6 days after hatching, from the lung of the mouse. Transverse section through the intestinal region.

Fig. 8. Embryo after incubation of the egg for 35 days, artificially hatched. Anterior portion of the body.

LETTERING.

e.c., excretory canal. *d.l.*, dorsal line. *d.p.*, dorsal papilla. *l.c.*, lateral canal. *l.l.*, lateral line. *l.m.*, lateral membrane. *n.e.c.*, nucleus of excretory cell. *o.*, oesophagus. *o.b.*, oesophageal bulb. *r.l.l.*, right lateral line. *s.c.*, subcuticle. *s.k.*, skeletal rod. *s.v.p.*, subventral papilla. *v.l.*, ventral line. 1, external layer of the cuticle. 2, midlayer of the cuticle. 3, internal layer of the cuticle.

A REVISION OF THE GENUS *FASCIOLA*.

WITH PARTICULAR REFERENCE TO *F. GIGANTICA* (COBBOLD) AND *F. NYANZI* (LEIPER).

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(With Plate III and 4 Text-figs.)

The material which is the subject of this paper was obtained from the following sources.

One tube of flukes collected by Dr H. H. Marshall at Bassein and Rangoon, British Burmah (referred to below as "Rangoon specimens")[1]; two tubes sent by Mr H. E. Hornby at different times from Northern Rhodesia (referred to as "Rhodesia specimens," "1st collection" and "2nd collection" respectively); and two tubes (Nos. 29 and 65) from the Veterinary Pathology Laboratory, Nairobi, British East Africa, collected by Mr R. E. Montgomery (the former referred to as "Nairobi specimens")[1]; in all comprising 40 species. I am very much indebted to Dr C. L. Boulenger, F.Z.S., Professor of Zoology at Lahore, for entrusting me with the description of this material.

The tubes contained elongated flukes of the genus *Fasciola*. It was found on examination that all the specimens (with the exception of those contained in the tube, Nairobi, No. 65) were related to *Fasciola gigantica* (Cobb.) and the question of the relationship of the various elongated flukes, that have been described from time to time under different specific names, with Cobbold's species and these new specimens, was thus raised again.

The question may be stated thus—do all these forms belong properly to *F. gigantica* (Cobb.) or should they be split up into more than one species? The history of the matter can briefly be told[2]. *F. gigantica* was described by Cobbold (1856) from specimens found in a giraffe belonging to a travelling menagerie.—Railliet (1895) communicated the discovery of an elongated fluke in Senegal cattle, slaughtered at St Louis and provisionally named it *F. hepatica* var. *angusta*.—Looss (1896) described a fluke from cattle slaughtered at Cairo that he named *F. hepatica* var. *aegyptiaca*, but which he considered a distinct species in 1899.—Blanchard (1896) suggested that both these varieties were in reality the same as Cobbold's *F. gigantica* but he gave no evidence or figures to support this suggestion.—Looss (1902) returned to the subject after examining a large number of specimens from

[1] Received from the Quick Laboratory, Cambridge.

For detailed discussion of the earlier history and complete bibliography see Stiles 1894–95.

the Cairo abattoirs. He accepts Blanchard's suggestion and withdraws the species *aegyptiaca*, not entirely without misgivings[1], and further suggests that the *gigantica* type of fluke is an African form in the same way as *F. magna* may be looked upon as an American form. In this note he gives, however, no anatomical details and no figures.—Braun (1906), without adding any original observations, is willing to accept the identity of *F. angusta* and *F. aegyptiaca* with one another but is sceptical of their identity with *F. gigantica*.

The prevailing uncertainty on the subject is largely due to the imperfect description of *F. gigantica* given by Cobbold and the fact that it has not been added to or revised since his time. By the courtesy of Dr Arthur Keith, F.R.S., I was given facilities for examining the original specimens in the Royal College of Surgeons, and am able to record all that the state of preservation of the specimens will allow to be contributed towards the elucidation of this matter. The specimens are three in number and quite extraordinarily different. They will be described in order of size:

COBBOLD'S *FASCIOLA GIGANTICA*.

Specimen No. 1 (Text-fig. 1). 76 mm. long by 5 mm. at broadest part. Cone cylindroconical and mounted on sharply projecting "shoulders," the left in this specimen being more anteriorly placed than the right. The ventral sucker is large and prominent with an irregular triangular aperture. The greatest breadth of the body is attained just behind the right "shoulder" and it narrows so slightly that it has only decreased 1 mm. at the posterior end of the testis area—a length of 35 mm. from the mouth. The tail is bluntly pointed and the last 41 mm. of the body are entirely occupied by yolk glands and alimentary canal. Narrow strips of yolk glands continue laterally to the "shoulders." The testes occupy the usual position and are coarsely lobed. The shell gland is visible 12 mm. from the anterior end and the uterus is long and loosely coiled. The gut cannot be made out in detail and no ramifications of the lateral diverticula can be seen. Yolk glands appear to spread on both sides of the gut. Spines are not visible. Proportion of length to breadth, 15·2 to 1.

Specimen No. 2 (Text-fig. 2) is 59 mm. long and 7 mm. broad. The cone passes into the body insensibly, there being no distinct "shoulders." The sides are almost parallel, tapering ever so slightly towards the tail, which is bluntly rounded. The testes occupy more space than in No. 1 and are coarsely lobed. The remainder of the organs which can be made out are typical, or as figured by Cobbold. I make out, however, more than 8–10 branches of the gut diverticula and indeed Cobbold's statement conflicts with his figures in this respect. Size of eggs: length 0·145 mm. to 0·150 mm., breadth 0·082 mm. to 0·088 mm. Proportion of length to breadth over 8 to 1.

[1] "...Ich wüsste gegen die Berechtigung seines Vorgehens gegenwärtig nichts mehr einzuwenden, und ziehe *F. aegyptiaca* als selbständige Species zurück."

Specimen No. 3, 23 mm. long by 3·5 mm. broad, is a small fluke of similar proportions to No. 2, but the cone is larger in proportion to the body. The condition of the specimen makes it difficult to determine. The uterus is large and with few coils; it contains some eggs. The space occupied by the testes is unusually large, from the mouth to the posterior border of the testis area measuring about 18 mm. The ventral sucker is not prominent. It is not possible to make out the alimentary canal. The yolk glands are normally arranged and the median commissures to the shell gland are visible. Proportion of length to breadth under 7 to 1.

Text-fig. 1

Text-fig. 2

Specimen No. 2 is a type of the specimen figured by Cobbold but somewhat longer in proportion to the breadth than his figure. The average length of his specimens is given as 2 inches and as this type specimen is nearly $2\frac{1}{2}$ inches it may be taken as slightly larger than the average. In the largest specimen (No. 1) the proportion of length to breadth is amazingly larger than any known fluke, and in the other specimens it is remarkably large. One can only look on the classing of these three worms in one species with grave suspicion until similar specimens are again found in the giraffe and their anatomy is accurately described.

In the meantime the medium sized specimen (No. 2) must be taken as the type of *Fasciola gigantica*.

The material in my possession which bears on the specimens under consideration is described below, but only the important features are recorded.

RANGOON SPECIMENS (Pl. III, fig. 1).

Largest 45 mm. by 12 mm. Narrowest 8 mm. by 34 mm. Shortest 29 mm. by 9 mm.

The large cone passes insensibly into the body; in no case are "shoulders" more than slightly indicated. The body in every specimen tends to expand slowly to its greatest width at or about the posterior border of the testis area and ends in a very bluntly rounded tail. The ventral sucker is round and

prominent and its lumen is produced posteriorly into a triangular pouch. The pharynx is long and the oesophagus very short, the diverticula of the gut are very strongly branched externally and internally, and the internal branches are ramose. Yolk glands spread on both sides of the alimentary canal. The testis area is moderately large, its posterior margin being about one-third of the entire length from the tail. The ovary is on the right side and, as in all other points of the histology and finer anatomy, is similar to *F. hepatica*. The body is very flat dorsoventrally and covered with moderately large spines. The eggs are of sizes lying between 0·140 mm. to 0·160 mm. in length and 0·060 mm. to 0·100 mm. in breadth. Average proportion of length to breadth 3·2 to 1.

Locality. Cattle, Bassein and Rangoon.

RHODESIA SPECIMENS (Text-fig. 3). 1*st Collection*.

Longest 39 mm. by 11 mm. Shortest and narrowest 36 mm. by 10 mm. Broadest 12 mm. by 37 mm.

These resemble the Rangoon specimens in general form, but the body reaches its greatest length nearer to the anterior end and tapers very gradually to a blunt tail. The ventral sucker has a triangular aperture and is slightly pouched posteriorly. The general anatomy is as above. The body is very flat dorsoventrally and the spines are moderately large.

Eggs: length 0·150 mm. to 0·170 mm., breadth 0·070 mm. to 0·085 mm. Average proportion of length to breadth 3·3 to 1.

Locality. Cattle, Northern Rhodesia.

RHODESIA SPECIMENS (Text-fig. 4) 2*nd Collection*.

Longest 37 mm. by 9 mm. Widest 13 mm. by 26 mm. Shortest 25 mm. by 10 mm. Narrowest 8 mm. by 36 mm.

The majority of these specimens are more slender than any described above. The slenderness of the body gives the cone an appearance of large size—it is perhaps larger in proportion to the body than in the specimens already described. The "shoulders" are very slight. The body soon reaches its full width and retains it for one-third of its length, tapering posteriorly to a bluntly pointed tail. The anatomy is as above.

Eggs: length 0·130 mm. to 0·175 mm., breadth 0·075 mm. to 0·090 mm. Average proportion of length to breadth 3·7 to 1. In many specimens the proportion is over 4 to 1.

Locality. Cattle, Northern Rhodesia.

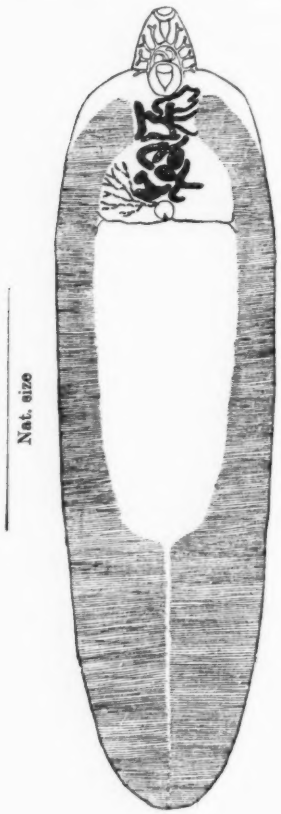
NAIROBI SPECIMENS (Pl. III, fig. 2).

Three specimens measuring 33 mm. by 7 mm., 35 mm. by 6 mm., and 34 mm. by 6 mm. and differing in slight points from those described above. The body is very slender and the large cone is, at its base, as wide as the body, no "shoulders" being present. It expands slightly for about one-third

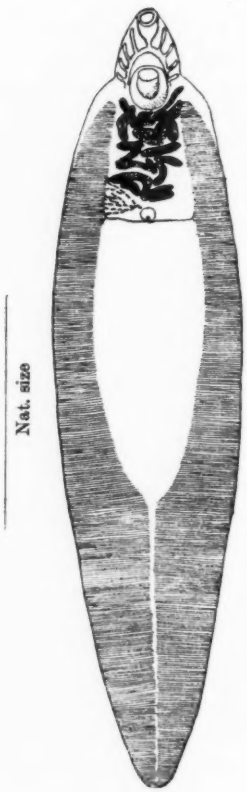
of its length and then tapers to a bluntly pointed tail. The ventral sucker is very large and protuberant and has a deep posterior pouch. The oesophagus is about half as long as the pharynx. Large spines cover the body, and smaller ones the cone. Average proportion of length to breadth 4·7 to 1. The anatomy is as above.

Eggs: length 0·125 mm. to 0·155 mm., breadth 0·075 mm. to 0·095 mm.

Locality. Ox, British East Africa.



Text-fig. 3



Text-fig. 4

DISCUSSION AND CONCLUSIONS.

The relationship of the flukes described above to those already described by Railliet and Looss admits of little doubt.

The Rangoon specimens can be seen at once to correspond in almost every detail with Looss' *F. aegyptiaca*; the only difference to be found is in the slightly narrower proportions, on the average, of Looss' specimens.

Similarly the Nairobi specimens can be referred to the variety originally described by Railliet under the name of *F. hepatica* var. *angusta*, from which they only differ in the slightest degree. The Rhodesian flukes possess no character which would separate them from either, the first collection coming nearer to the Rangoon specimens and the second collection to the Nairobi specimens.

The bridge between the two forms being thus complete, it may be taken that *F. angusta* and *F. aegyptiaca* are one and the same species.

Their relation to *F. gigantica* is less obvious. The great size of Cobbold's specimens may partly be accounted for by the undoubted maceration they had undergone before examination. Goddard (1919) records cases of extreme alterations in *Fasciolopsis*, measured immediately after evacuation and after standing a few hours in water. Shape and size cannot count for a great deal in the delimitation of species in these forms, owing to the distortion inevitably produced by maceration and fixation, unless coupled with distinct anatomical differences.

The anatomy provides us with little on which to base a separation. The alimentary canal is provided with the ramose internal branches of the diverticula, which have been shown to be characteristic of all the forms described above.

Cobbold's figures do not distinctly show the proportion of pharynx to oesophagus, but it is indistinctly indicated (it was not possible to make out the point in the original specimen I examined) that the oesophagus is quite as long as the pharynx. If this is correct—and the mobility of the muscular pharynx makes the character at least of doubtful value—it makes a point of difference from these recent specimens. The testes are similar and occupy a similar proportion of body space. The remaining organs are similar. The parasite comes from the same continent as all the elongated forms (except the Rangoon specimens) that have been hitherto described.

The eggs—length 0·145 mm. to 0·150 mm., breadth 0·082 mm. to 0·088 mm. lie within the limits of those of the specimens described above.

On the whole therefore the differences amount to so little that we may, without much hesitation, refer all these forms to the species *Fasciola gigantica* (Cobbold).

The descriptions given above may now be combined to make the following diagnosis of *F. gigantica*.

F. GIGANTICA (COBB.).

Body elongated and at least three times as long as broad. Cone passing almost insensibly into the body, prominent "shoulders" always being absent. As a rule the sides of the body are roughly parallel and the posterior extremity is bluntly rounded or more rarely bluntly pointed. The ventral sucker is large, often protuberant and its cavity is usually prolonged backwards into a blind pouch. The pharynx is longer than the oesophagus. The external branches of

the diverticula of the alimentary canal are as in *F. hepatica*, the internal branches, however, are numerous and always ramose to a greater or less extent. The yolk glands are present on both sides of the alimentary canal. The testis area is shorter in relation to the rest of the body than in *F. hepatica*.

The eggs are larger than those of *F. hepatica*, varying from 0·125 mm. to 0·175 mm. in length to 0·060 mm. to 0·100 mm. in breadth.

Habitat. Liver of ruminants.

Looss' observation that in this species we have to do with an African liver fluke in the same way as *F. magna* may be called an American fluke, must be looked upon with caution, until it is known whether the Rangoon specimens indicate a wider distribution than he had reason for suspecting.

FASCIOLA NYANZI (LEIPER) (Pl. III, figs. 3 and 4).

This fine species was found by Leiper in the bile ducts of the liver of a hippopotamus taken in Uganda and described by him under the above name (1910). His specimens were somewhat macerated and he was therefore unable to describe the species in every particular. Among the material from Nairobi (tube No. 65) I fortunately found a number of well preserved specimens of this species and I am able to add to Leiper's original description.

None of the specimens were as large as the largest described by Leiper, the longest being 59 mm. by 9 mm., the broadest 13·5 mm. by 49 mm. and the smallest specimen 35 mm. by 4·5 mm., but the remarkable general form was unmistakably as he described it. The species is especially noticeable for the great breadth of the "shoulders," the large cone and the long tapering body, almost entirely occupied by yolk glands.

The worm is thickly covered with spines, of a moderate size on the body and smaller and more closely set on the cone. The oesophagus is exceedingly short and the paired diverticula of the gut approximate behind the level of the shell gland and for the rest of their course lie very close together. The internal branches of the diverticula are fairly numerous, but small and infrequently branched. Branches from opposite sides frequently pass across one another or lie close together, giving a superficial appearance of anastomosis. The testes are confined to the anterior third only of the body. The ovary lies on the right hand side of the animal and is a typical branched body. The uterus is short and its coils are close behind the ventral sucker. Laurer's canal is present; it is very small and in the specimens examined had no contents. The yolk glands extend rather further forward into the "shoulders" in my specimens than in Leiper's, and lie exclusively (except for a stray branch or two) on the ventral side of the gut. It shares this interesting feature with *F. magna* in the genus *Fasciola*. The point is particularly easy to make out in the cleared specimens; viewed from the dorsal surface the alimentary canal is sharply outlined against a background of yolk glands.

The excretory and nervous systems are as in *F. hepatica*.

The eggs vary considerably in size in different specimens, and the size

given by Leiper (0·150 mm. by 0·070 mm.) must be taken as a minimum. Extracted from the uterus and measured in 70 per cent. alcohol the eggs lie between 0·150 mm. to 0·190 mm. in length and 0·070 mm. to 0·110 mm. in breadth. Measured from balsam preparations the eggs are on the average smaller (through shrinkage) than those extracted and measured in the medium in which the flukes are preserved.

SUMMARY.

1. The specimens in the material here dealt with make a series of forms connecting *F. angusta* (Railliet) and *F. aegyptiaca* (Looss).

2. No important character separates any of these flukes from *F. gigantica* (Cobbold) and they must accordingly be all identified with this species.

3. The following key represents the simplest method of distinguishing between the species of *Fasciola* at present described. (For detailed diagnoses see the literature referred to below and this paper.)

(1) Yolk glands ventral to gut . . . . . 2.
Yolk glands on both sides of gut. . . . . 3.

(2) Body very large and thick; cone not very distinct; oesophagus one and a half to three times as long as pharynx . *F. magna.*
Body slender and awl shaped; cone very large and distinct; oesophagus exceedingly short . . . . . *F. nyanzi.*

(3) Body at least three times as long as broad; "shoulders" absent or indistinct; internal branches of gut numerous and branched *F. gigantica.*
Body broad and leaf shaped; cone sharply set off from body on wide "shoulders"; internal branches of gut few and little if at all branched . . . . . *F. hepatica.*

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EXPLANATION OF PLATE III.

The lateral extent of the yolk glands is shewn in each figure by shading. Only the broad plan of the external branches of the diverticula of the gut is indicated, the fine terminal arborisations being omitted.

Fig. 1. *Fasciola gigantica* (Cobbold). Ventral view.
Fig. 2. „ „ „ Ventral view.
Fig. 3. *Fasciola nyanzi* (Leiper). Anatomy, from ventral view.
Fig. 4. „ „ „ External features; ventral.

EXPLANATION OF LETTERING.

a.s.—anterior sucker and mouth; *ov.*—ovary; *ph.*—pharynx; *sh. gl.*—shell gland; *T.*—testis area; *ut.*—uterus; *v.s.*—ventral sucker; *y.g.*—yolk gland area.

Fig. 1

Fig. 2

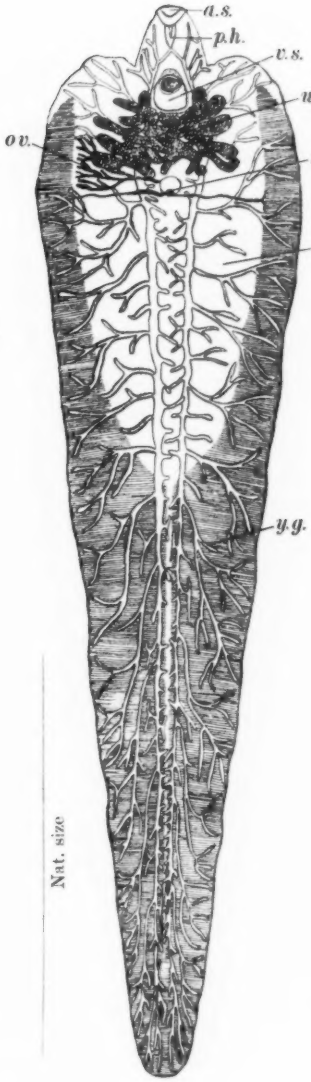

Fig. 3

Fig. 4

A NEW GENUS OF NEMATODES PARASITIC IN ELEPHANTS.

By H. A. BAYLIS, M.A.

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(With 7 Text-figures.)

A RE-EXAMINATION of the type-specimens of "*Sclerostoma*" *clathratum* Baird from the African elephant, which are in the British Museum, has led to a rather interesting discovery. The material was contained in two bottles, labelled in Baird's own handwriting. One bore the name "*Sclerostoma clathratum* Baird," and contained a single male specimen of the form now known as *Grammocephalus clathratus*. The other bottle was labelled "*Sclerostoma clathratum* Baird, ♀," and proved to contain worms of both sexes and of quite a different type from *Grammocephalus*.

It is somewhat remarkable that the curious figure given by Baird (1868) of the head of *Sclerostoma clathratum* has called forth little or no comment from subsequent writers. The fact appears to be that Baird had confused two quite distinct species, belonging to widely different genera, and the figure of the head (*l.c.* Fig. 2 *a*) as also the figures of the supposed female, do not belong to the same form as the enlarged figure (2 *c*) of the male tail, which is that of the *Grammocephalus* of recent authors.

The species taken for the female of *S. clathratum* by Baird appears to be a worm of Spirurid affinities, and is clearly very closely related to the "*Filaria*" *smithii* of Cobbold (1882), from the Indian elephant. Unfortunately it has not been possible to procure specimens of the latter form for comparison; but through the kindness of Lt.-Col. Clayton Lane material belonging to a very similar species from the Indian elephant has been placed at the writer's disposal, and on comparison of this and Baird's material with Cobbold's description and figures it seems clear that all three species belong to one and the same genus.

Railliet, Henry and Bauche (1914) have noted the Spirurid affinities of *Filaria smithii*, and have named it provisionally *Spiroptera smithii*, using the name *Spiroptera* in default of a clearer definition of its position. The genus to which these worms belong seems to the writer to have very close relationships with *Habronema*, Diesing, and may be defined as follows:

PARABRONEMA, n.g.

Spiruridae: Polymyarian worms, having the mouth bordered by paired lateral lips, externally to which there are a dorsal and a ventral shield of cuticle. Each lip bears one large, median lateral papilla and a pair of small sublateral papillae. Of the dorsal and ventral shields, each carries a pair of larger papillae (Figs. 1, 4, *p.*), situated at some distance behind the extremity of the head. The cuticle of the head is thick, and folded in a complicated manner so as to form a circlet of six horseshoe-shaped auricular appendages (Figs. 1, 4, *a.*), of which two are lateral, two subdorsal and two subventral. The open anterior end of the horseshoe is partly filled up by a vesicular swelling of the cuticle. The edge of each of these appendages is further folded to form a groove somewhat resembling the cervical grooves or "cordons" of the *Acuaria* group.

The body is rather slender, tapering rather more in front than behind. The cuticle shows more or less distinct transverse striations. The buccal cavity, at a short distance from the oral aperture, is elongated transversely in a direction at right angles to the sagittal plane, and then passes into a long, cylindrical, cuticular tube (Figs. 1, 4), with thick walls. The oesophagus (Fig. 1, A) consists of a short, narrow, anterior portion and a long, somewhat wider, posterior portion, both portions being muscular. The anterior portion is surrounded by the nerve-ring. The minute excretory pore is situated at about the level of the nerve-ring, and a pair of cervical papillae (Fig. 1, A, *c.p.*) with bristle-like terminations a little further back.

The tail of the male is coiled ventrally into a spiral, provided near the extremity with lateral alar expansions, and largely covered on the ventral surface with interrupted, longitudinal cuticular ridges (Fig. 2). The spicules (Figs. 3, 6) are markedly unequal, the slender left spicule being from two to four times as long as the right, which is rather stouter. A small, somewhat triangular accessory piece is present (Figs. 3, 6). The paired caudal papillae have long nervous pulps, and are present to the number of six pairs, of which four are preanal and two postanal. The arrangement of the corresponding papillae of the two sides is somewhat asymmetrical. The anterior pair of postanal papillae (Figs. 2, 5) present a remarkable peculiarity, lying transversely across the ventral surface, the left a little in front of the right, with their terminations either passing beyond, or at least close to, the mid-ventral line of the tail. In addition to the paired papillae, a large median double papilla is present immediately in front of the cloacal aperture.

The female is considerably larger than the male. The tail is short, conically pointed or blunt, and characteristically curved towards the dorsal side. The vulva is situated almost immediately behind or in front of the posterior end of the oesophagus. The vagina is long, narrow and muscular, and runs straight backwards with the exception of a curious little U-shaped bend in its course (Fig. 7) at a short distance from the vulva. The two uterine branches are

parallel, running backwards at first, one of them returning towards the anterior end of the body, the other continuing posteriorly. The worms are apparently viviparous, the uterus containing immense numbers of embryos which are not enclosed in a hard egg-shell.

Hab. stomach[-wall] of elephants.

1. **Parabronema indicum,** sp.n. (Genotype.)

(Figs. 1–3.)

For measurements see Table, p. 65.

This is a rather small form, in which the head (Fig. 1) is of a conical shape, distinctly narrower in front than at the back of the auricular appendages. The latter (Fig. 1, *a.*) are regularly horseshoe-shaped, and bear a narrow groove on their free edges. The borders of the lips (Fig. 1, C) are simple, without a well-marked median inward projection. The anterior pair of postanal papillae (Fig. 2) in the male overlap in such a way that the termination of the right papilla is well to the left of the mid-ventral line. The posterior pair of postanal papillae are symmetrically placed opposite to each other. The two terminations of the large median preanal papilla appear to be situated near its lateral limits. The left spicule is very slender, and is nearly three times as long as the right.

The female is about twice as large, on an average, as the male. The tail is conical, with rather blunt tip. A pair of caudal papillae are just visible as minute dimples in the cuticle close to the tip. The vulva is situated a little behind the posterior end of the oesophagus. The vagina forms a U-shaped bend at about 0·25 mm. from the vulva. After a further course of about 0·4 mm. it widens into a fusiform swelling, which gives off the two uterine branches posteriorly. The uterine branches themselves also have small fusiform enlargements near their origin. One branch runs back to a point about 0·35 mm. from the anus, where it turns forward again. The other turns forward sooner, and runs up nearly as far as the posterior end of the oesophagus, where it forms a loop and runs once more posteriorly.

This species differs from *P. smithii,* as described by Cobbold and by Mitter (1912), chiefly in its somewhat larger size, in the greater absolute length of the spicules of the male, and in the greater relative length of the left spicule. It also differs in the number and arrangement of the caudal papillae of the male; but it may be taken as almost certain that some of these papillae were overlooked by Cobbold, and that a re-examination of the species would show that their arrangement agrees with that in the forms here described.

Host. The type-material, now in the British Museum (Natural History), was collected from the stomach-wall of an Indian elephant (*Elephas indicus*)[1] by the Superintendent, Civil Veterinary Department, Madras.

[1] The writer is informed by Mr Oldfield Thomas, F.R.S., that the more correct name of the Indian elephant is *E. maximus,* and that of the African elephant *Loxodonta africana.* In the present paper, however, the more familiar names have been retained.

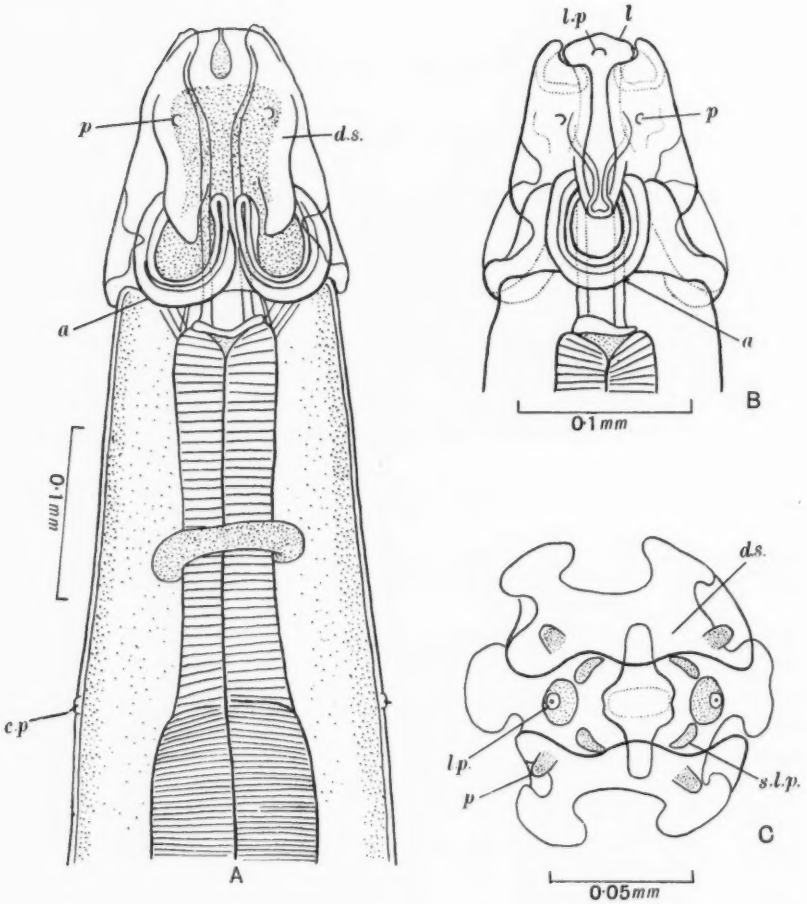

Fig. 1. *Parabronema indicum.* A, dorsal view of head and neck; B, lateral view of head; C, extremity of head, seen from the front. *a.*, *a.*, auricular appendages; *c.p.*, cervical papilla; *d.s.*, dorsal shield; *l.*, lip; *l.p.*, lateral papilla of lip; *p.p.*, papillae of dorsal and ventral shields; *s.l.p.*, sublateral papilla of lip.

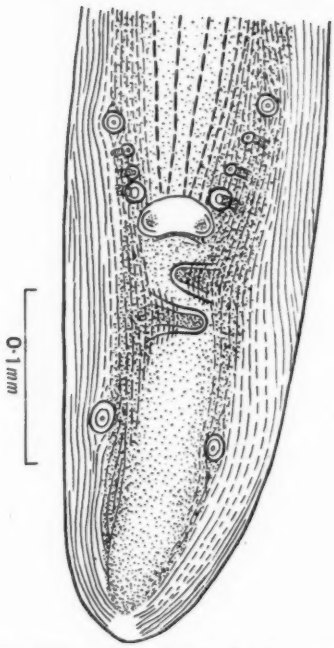

Fig. 2. *Parabronema indicum*. Tail of male; ventral view.

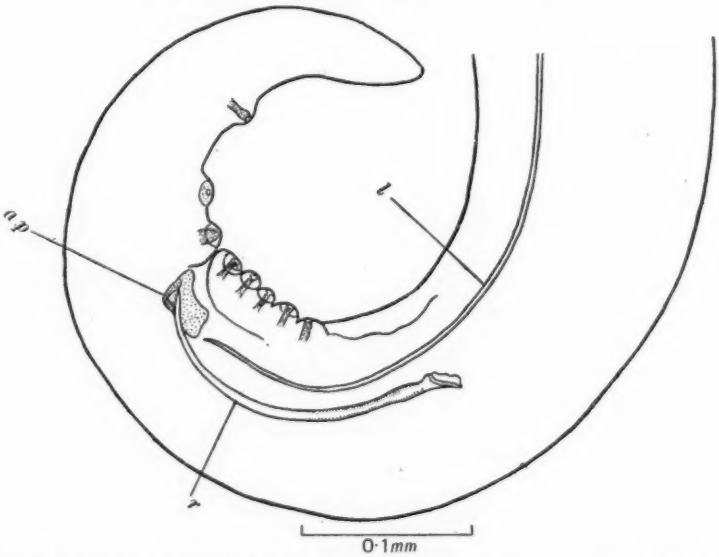

Fig. 3. *Parabronema indicum*. Tail of male; lateral view. *a.p.*, accessory piece; *l.*, left spicule (terminal portion); *r.*, right spicule.

2. **Parabronema africanum,** sp.n.

(Figs. 4–7.)

Sclerostoma clathratum (♀) Baird (1868), p. 262; Figs. 2 ♀, 2 *a*, 2 *b*.

For measurements see Table, p. 65.

This is a much larger form than the preceding, and the inequality in size between the sexes is less marked, the male attaining about two-thirds of the

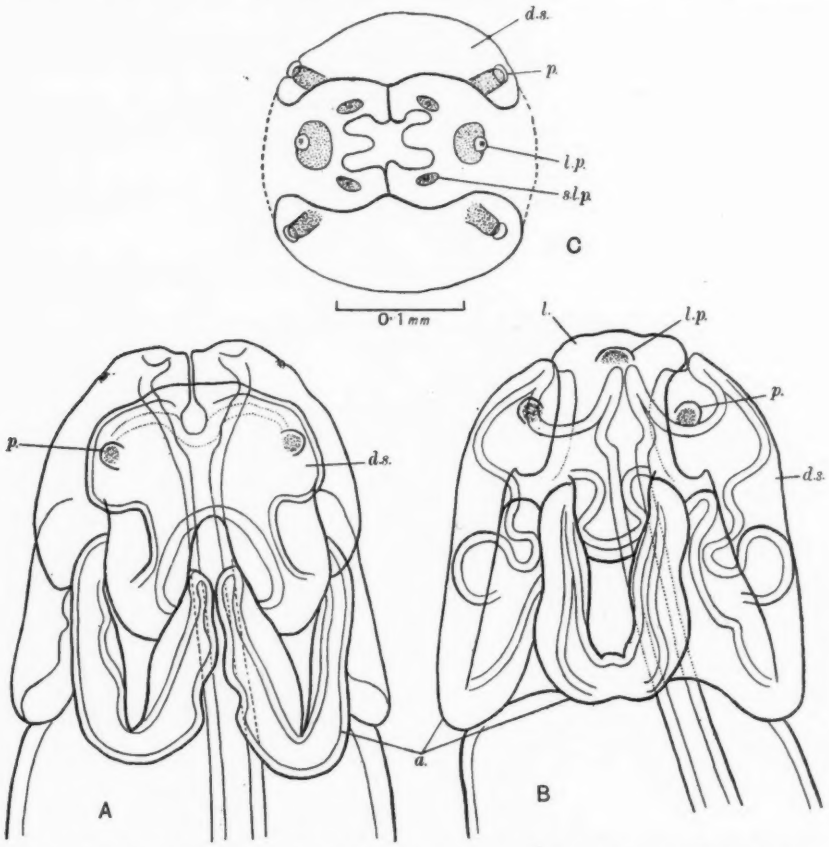

Fig. 4. *Parabronema africanum.* The head. A, dorsal view; B, lateral view; C, the extremity, seen from the front. *a.*, auricular appendages; *d.s.*, dorsal shield; *l.*, lip; *l.p.*, lateral papilla of lip; *p.p.*, papillae of dorsal and ventral shields; *s.l.p.*, sublateral papilla of lip.

length of the female. The male, however, is easily distinguished by the well-marked spiral coiling of the tail, and it is rather astonishing that Baird did not suspect an error when he described the tail of the female *S. clathratum* as "*obtusa, saepe convoluta.*"

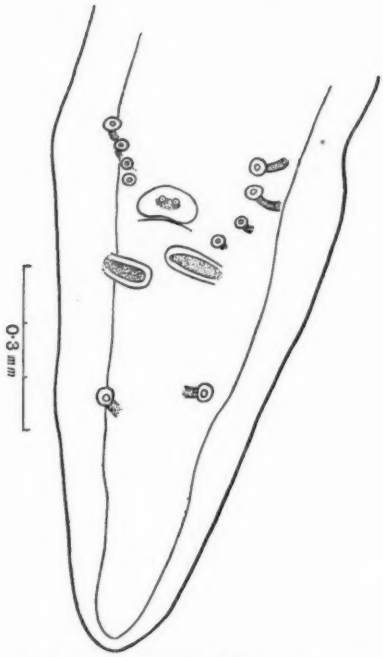

Fig. 5. *Parabronema africanum*. Tail of male; ventral view.

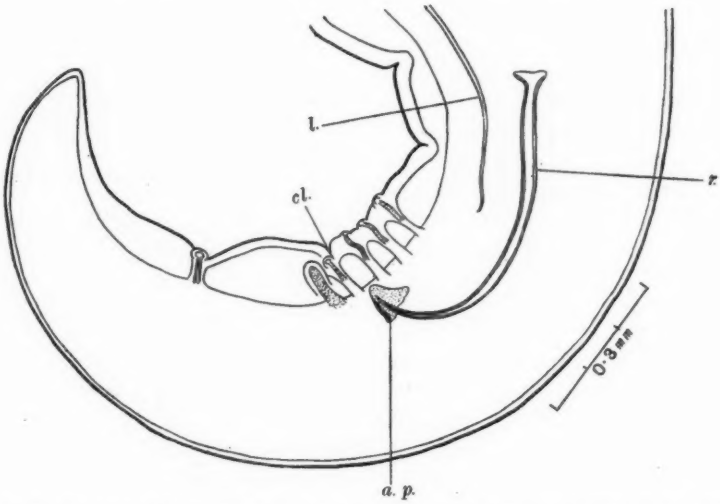

Fig. 6. *Parabronema africanum*. Tail of male; lateral view. *a.p.*, accessory piece; *l.*, left spicule (terminal portion); *r.*, right spicule.

The cuticle, especially near the head, shows the minute longitudinal striations, in addition to the usual transverse striations, which suggested to Baird the name *clathratum*.

The head (Fig. 4) is almost invariably bent towards the dorsal side, and may be roughly described as bullet-shaped. It is nearly as wide at the level of the outer papillae as at the back of the auricular appendages. The latter (of which there are six, and not five, as stated by Baird) are somewhat elongate, with their edges curled inwards so as to form a nearly V-shaped aperture, and their "grooves" are very wide, and carried on the inner surface.

The lips (Fig. 4, C) have a median inward projection on their opposed edges, with deep incisions on either side of it, so that the outline of the mouth is somewhat X-shaped. The cervical papillae are situated in little cuticular pits, from which their minute bristle-like terminations project.

The caudal papillae of the male (Figs. 5, 6) are distinctly asymmetrical, the group of four preanal papillae on the left side being much more widely separated than those on the right, so that the most posterior of the group lies at the level of the cloaca. The terminations of the anterior postanal

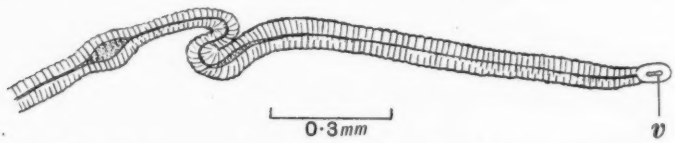

Fig. 7. *Parabronema africanum*. Terminal portion of vagina. *v*, vulva.

papillae do not quite reach the mid-ventral line of the tail. The two terminations of the median preanal papilla appear to be situated close together near the middle line. The left spicule is more than four times as long as the right.

The tail of the female is conical, with a rounded tip. Caudal papillae have not been observed. The vulva is situated either just behind or just in front of the posterior end of the oesophagus. The U-shaped bend of the vagina (Fig. 7) occurs at about 1–1·2 mm. from the vulva. Behind this point the vagina becomes narrower, still running straight backwards, and gradually widening, for a further distance of about 3·2 mm. before giving off the uterine branches, the course of which is probably similar to that described for *P. indicum*.

Host. The type-material was collected by Dr Murie from the stomach of a young African elephant (*Elephas africanus*) which died in London in 1867.

3. **Parabronema smithii** (Cobbold).

Filaria smithii Cobbold (1882), p. 237; Text-figs. 6–7; Pl. XXIV, figs. 7–10.
Filaria smithii Mitter (1912), p. 113; Pl., Figs. *e—g*.
Spiroptera smithi Railliet, Henry and Bauche (1914), p. 210 (*nec Filaria smithi* Sambon, 1907).

For measurements see Table, p. 65.

Practically the only distinctive features for this species that can be gathered from Cobbold's description are those of size. As has been pointed out above,

when dealing with *P. indicum*, the number and arrangement of the male caudal papillae cannot, probably, be regarded as satisfactorily described. The *two* rows of translucent auriculate appendages of the head referred to by Cobbold may probably be interpreted as corresponding to (*a*) the auricular appendages themselves, and (*b*) the vesicular swellings of the cuticle which partly fill their cavities in front, in the two forms now described. The account given of the cephalic papillae is not very clear, while nothing corresponding to the minute papillae said to exist within the concavity of the auricular appendages has been observed in *P. indicum* or *P. africanum*. Mitter (1912) adds little to Cobbold's description.

Host. Cobbold's material was collected from the coats of the stomach of *Elephas indicus*, where the worms inhabited tumours of about the size of a filbert nut and of an oval, flattened shape. A similar habitat is indicated by Mitter, who, however, mentions the "intestines," not the stomach.

Table of measurements of the species of Parabronema.

(All measurements are in millimetres, and represent specimens of about the maximum size. The figures for *P. smithii* have been calculated from the fractions of an inch given by Cobbold, and are only approximate.)

	Species					
	indicum		*africanum*		*smithii*	
	♂	♀	♂	♀	♂	♀
Length	7·9	13·0	40·0	57·0	4·2*	8·5*
Thickness (maximum)	0·31	0·39	0·8	1·0	0·2	0·25
Diameter of head at posterior end of auricular appendages	0·14	0·15	0·27	0·32	—	—
Length of tail	0·17	0·32	0·85	0·52	—	—
Length of buccal cavity	0·17	0·18	0·35	0·4	—	—
Distance from anterior extremity to posterior end of auricular appendages	0·15	0·17	0·3	0·36	—	—
Distance from anterior extremity to posterior end of cervical papillae	0·39	0·42	0·7	0·85	—	—
Distance from nerve-ring	0·32	0·34	0·7	0·83	—	—
Distance from excretory pore	0·33	0·35	?	0·9	—	—
Distance from junction of two divisions of oesophagus	0·4	0·4	0·9	1·0	—	—
Distance from posterior end of oesophagus	2·2	2·25	6·5	7·2	—	1·5
Distance between transverse striations of cuticle	0·0035		0·01		—	
Length of spicules	R. 0·39 L. 0·93		R. 0·68 L. 3·15		Shorter 0·18 Longer 0·32	
Greatest length of accessory piece	0·06		0·08		—	
Distance of vulva from posterior end of oesophagus	0·4		0·1 in front, 0·2 behind		[Probably about 0·2 behind]	
Distance from caudal papillae (♀) to tip of tail	0·03		—		—	

* Mitter (1912) gives 4·16 mm. for the length of the male and 8·3 mm. for that of the female of *Filaria smithii*.

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SOME OBSERVATIONS AND EXPERIMENTS ON INSECT FLAGELLATES, WITH SPECIAL REFERENCE TO ARTIFICIAL INFECTION OF VERTEBRATES.

(A REPORT TO THE DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH[1].)

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(*From the Wellcome Bureau of Scientific Research.*)

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I. OBSERVATIONS ON *CRITHIDIA MELOPHAGIA* AND ITS RELATION TO THE SHEEP-TRYPANOSOME.

Woodcock (1910) discovered a trypanosome naturally occurring in the blood of British sheep. This finding was confirmed by Behn (1911, 1912) in Germany. In both cases the authors did not give any description of the parasite, which was seen by them only in single cases, and they failed to cultivate the trypanosomes.

According to Woodcock (1910) the trypanosome represents a developmental stage of *Crithidia melophagia* Flu, 1908, parasitising the gut of the sheep-ked, *Melophagus ovinus*. As the "ked" is a typical blood-sucking insect, and the degree to which it may be infected with these flagellates

[1] The observations here described were made at the Wellcome Bureau of Scientific Research with the aid of a grant from the Department of Scientific and Industrial Research. I take this opportunity of offering my warmest thanks to the Director of the Bureau, Dr Andrew Balfour, C.B., C.M.G., for his hospitality and kind assistance, and to Dr C. M. Wenyon, C.M.G., C.B.E., M.B., B.Sc., who has given me unfailing help and valuable advice in the course of my work. I am also indebted to Dr Wenyon for performing the inoculations for me, as I had not at that time obtained a Licence for such experiments.

frequently reaches 100 per cent., such a supposition was quite natural, although direct evidence of any connection between the said flagellate and the sheep-trypanosome was lacking.

Later, the morphology and life-history of *Crithidia melophagia* in the gut of the sheep-ked were described in detail by Swingle (1909) and Porter (1910), who arrived at the conclusion that it was a specific insect parasite. This seemed the more obvious to the authors since both they and Flu (1908) had discovered that infection in the "keds" was transmitted hereditarily, so that the necessity of a second host, the sheep, seemed to have been eliminated.

Swingle (1911, 1911*a*) tested this view experimentally. He examined the blood of a great number of sheep; inoculated them with, and fed them on, the contents of sheep-keds' guts infected with these flagellates, and put freshly hatched "keds" on sheep previously washed in an antiseptic solution. All these experiments gave negative results, with the exception of two cases, in which young "keds" which showed no flagellates became infected with them after having lived on sheep for twelve days. This occurrence, however, the author explained as hereditary infection of the "keds."

Swingle's experiments were conducted so exhaustively that the question regarding the presence of trypanosomes in sheep and their relation to the flagellates of the sheep-ked seemed to have been finally solved.

There remained, however, several points which were not quite clear, and there were other methods by which the problem could be further investigated.

The first point that required further elucidation was the alleged hereditary transmission of *C. melophagia*. Hereditary infection was described by Flu (1908), Swingle (1909) and Porter (1910) as the means by which infection is maintained in the sheep-keds.

The second question to be solved was the possibility of cultivating the supposed trypanosomes from the sheep's blood. The negative results of numerous blood examinations made by Pfeiffer (1905), who was the first to describe *C. melophagia* Flu (1908), Swingle (1911, 1911 *a*), and Porter (1910), and the scanty positive results obtained in the same way by Woodcock (1910) and Behn (1911, 1912) showed that, even if trypanosomes occur in the sheep's blood, their number is so small that in most cases they escape detection. Now, it was shown by Crawley (1909, 1909 *a*, 1912) that it is possible to cultivate trypanosomes from the blood of cattle in which the ordinary examination of blood failed to reveal their presence. Stockman (1910) also discovered trypanosomes in British cattle which had hitherto escaped detection, and the observation has been confirmed by other authors.

Having these points in view, and taking into account the general importance of this question, both from the theoretical and practical aspect, since the presence of even a slight trypanosome infection might, under favourable conditions, be capable of producing a serious disease in sheep, as in the case of other domestic animals similarly infected, I have endeavoured to test this question experimentally.

Unfortunately, on account of the difficulty of obtaining live "keds," owing to the operation of the dipping laws in England, my experiments could not be conducted on as wide a scale as desired, but had to be limited to the study of certain points in the life-history and behaviour of *C. melophagia* and to attempts at culture of trypanosomes from the sheep's blood, and artificial infection of other mammals with these flagellates.

Whilst this work was in progress, several publications by Nöller (1917, 1919, 1919 *a*, 1920) came to hand from Germany. The author appears to have been studying this subject for several years. By using special culture media and methods, he succeeded not only in cultivating trypanosomes from the sheep's blood, but also in bringing about the transition from the crithidia forms to trypanosomes *in vitro*, thus establishing the identity of the two forms without any doubt. The trypanosome received the name of *Trypanosoma melophagium* Flu, 1908.

I had at my disposal four sheep[1], from which blood-cultures were made and kept at 24° C. and at 30° C., according to Nöller's methods (1919, 1919 *a*) in slightly alkaline bouillon. I did not succeed in cultivating any trypanosomes from the blood of these sheep, although they were infected with "keds" containing flagellates in their guts. As it was impossible to obtain new material, and especially very young lambs, experiments on which might have been more fruitful, I was compelled to postpone this part of the work in the hope of being able to continue it early in the spring, when conditions are more favourable.

As the morphology and development of *C. melophagia* in the gut of *Melophagus ovinus* have been studied and described in detail by other authors, I have directed my attention only to certain points that remained obscure in their description. One question is of especial importance. Flu (1908), Swingle (1909, 1911) and Porter (1910) claimed that these flagellates are transmitted to their offspring hereditarily, the flagellates penetrating into the ova, and thence into the developing embryo. The weak point in their description is the fact that the forms described and depicted by the three authors named have nothing in common with each other. Each author gives a different picture of the "hereditary" forms found, and with the exception of Porter's figures, most of them bear no resemblance to any of the forms which insect- or haemoflagellates usually assume. Porter claims to have actually seen the flagellate forms of the Crithidia penetrating through the eggs of the "ked," losing their flagella there and passing into the "resting stage."

I have examined a fair number of ova and pupae of the sheep-ked both in sections and in smears, and have employed Porter's technique in the latter case, but have failed to find any forms which could be interpreted as stages of a flagellate organism. In this respect my observations agree with those of Chatton and Delanoë (1912) and Cauchemez (1912), who have also failed to

[1] I wish to acknowledge my indebtedness to Mr J. B. Buxton, F.R.C.V.S., of the Wellcome Physiological Research Laboratories, for kindly supplying me with the necessary material for my work.

find any traces of hereditary infection in the sheep-ked. In several cases I saw structures which at first glance could be mistaken for flagella of the parasite, which, according to Porter, "are found floating freely in the vitellus of eggs." A careful examination of these structures, however, convinced me that they were spermatozoa, which find their way into the ovaries from the *receptaculum seminis*. It is a noteworthy fact that, although the authors named believed that hereditary transmission exists, they have all failed to find any traces of the flagellates thus inherited either in the larvae or in newly hatched "keds." Only after prolonged feeding on sheep's blood do the flagellates make their appearance in the gut of the young "keds." The natural deduction from such a fact would be the assumption of a possibility, at least, of infection from the sheep's blood, but the authors' conviction of the occurrence of "hereditary infection" leads them to suppose that in the larvae and newly hatched "keds" the flagellates are present in a cryptic stage, which is stimulated to final development by the ingestion of sheep's blood.

In order to throw some light on the relationship between *C. melophagia* and the sheep, I have made attempts artificially to infect mice with them.

In the course of these experiments I became interested in this question in general, and have extended the experiments to other vertebrates, using flagellates parasitising other insects also. These experiments are recorded in the second part of this paper, together with some observations on the vitality of *C. melophagia in vitro*.

II. EXPERIMENTS ON ARTIFICIAL INFECTION OF DIFFERENT VERTEBRATES WITH INSECT FLAGELLATES.

The possible pathogenicity of insect flagellates of the *Herpetomonas* type for vertebrates in which they do not naturally occur is interesting from several points of view. It may, on the one hand, throw light on the question of the phylogeny of the pathogenic haemo-flagellates—the trypanosomes and leishmanias; on the other hand it may serve to elucidate to a certain degree the rôle of insects as carriers and intermediate hosts in certain diseases in which such have not hitherto been found, *e.g.* in Kala-azar and Oriental Sore.

That trypanosomes and leishmanias have originated from purely insect flagellates which, by association of their hosts with vertebrates have gradually adapted themselves to life in the latter, is a hypothesis which, as far as trypanosomes are concerned, finds confirmation in the fact that the latter usually pass part of their life-cycle in some insect, the insect stages being similar to the forms of purely insect flagellates of the *Herpetomonas* group. As regards leishmanias, there is no direct evidence as yet of their connection with such forms, the only evidence of their relationship to the Herpetomonads being the flagellate forms they produce in cultures, the fact that they develop into flagellates in the stomachs of certain insects (Wenyon, 1911), and the very rare occurrence of such forms in the body of their vertebrate host (cf. Wenyon, 1914, 1915).

Recently, numerous works have appeared dealing with artificial infection of vertebrates with the flagellates of different insects both associated and unassociated with vertebrates. The majority of these are by Laveran and his collaborators, and Fantham and Porter. These observers claim to have proved that insect flagellates, when introduced into vertebrates, evoke in the latter symptoms of disease comparable to Leishmaniasis, and assume in them forms similar to the leishmania parasites.

I have repeated some of the experiments mentioned, and conducted others with new flagellates, but have failed entirely in producing any form of disease, or in finding any forms of the flagellates introduced into the animals experimented upon. These experiments have, however, led to certain observations on the vitality of the parasites thus introduced.

As the question of such artificial infection is of considerable interest, and important theoretical and practical conclusions have been deduced from them by the authors mentioned above, I propose to give a short description of my experiments, together with a brief review of the results arrived at by these authors.

The following are the species of flagellates with which such experiments had been made:

1. *Herpetomonas pattoni.*
2. *H. ctenopsyllae.*
3. *H. ctenocephali.*
4. *H. phlebotomi.*
5. *H. muscae-domesticae.*
6. ***H. calliphorae*[1].
7. **H. jaculum.*
8. *H. stratiomyiae.*
9. *H. pediculi.*
10. *Crithidia fasciculata.*
11. **C. melophagia.*
12. *C. tabani* (?)
13. *C. gerridis.*

For the sake of convenience I have reproduced, in Table I, the methods and results of experiments on artificial infection of vertebrates by various authors. As far as I could ascertain, this Table contains all the chief experiments on this subject (with the exception of some similar experiments on birds).

It can be seen from this Table that some of the workers have succeeded in introducing flagellates from insects into various vertebrates, and have evoked in them infections similar to Leishmaniasis, both as regards the morphology of their parasites and, in some cases, the lesions as well. Successful results were obtained with flagellates both from insects which are naturally associated with vertebrates and those which have no such association.

In the animals thus infected, the flagellates are said to make their appearance in the blood and organs in the form of leishmania and flagellate bodies. Infection of mice frequently terminates in death, and examination of organs *post mortem* shows that some of them (spleen and liver) are hypertrophied.

[1] Asterisks denote species which were used in my experiments as well; the species marked with two asterisks had not been used by previous workers.

Table I.

Experiments of different authors on artificial infection of vertebrates.

Species of flagellate	Host	Experimental animal	Mode of infection	Author	Results	Forms of parasites described in infected animals	Condition of infected animal	Remarks
1. *H. pattoni*	Rat-flea	Mice and Rats	per os	Laveran and Franchini, 1914 1914 *a*	+	Intracellular flagellates, free flagellates and leishmania forms in blood, liver, spleen and bone-marrow	—	Amongst the parasites were found leishmania forms with one nucleus and fusiform aflagellate forms. Cultures successful
2. *H. ctenopsyllae*	,,	Mice	,,	*Ibid.* 1914 *b*	+	Leishmania forms in blood and organs	—	Uninucleate leishmania forms found in blood and organs
3. *H. ctenocephali*	Dog-flea	(*a*) Guinea-pigs and mice	i.p. (cultures)	*Ibid.* 1920	+	Leishmania forms in blood and organs	Mouse infected from guinea-pig, died	Successful passage from guinea-pig to mouse
		(*b*) Mice	i.p.	*Ibid.* 1913	+	Leishmania forms in blood and peritoneal exudate	—	Most of the leishmania forms extra-cellular. Passages successful. Duration of infection 60 days
		(*c*) Mice, rat	i.p., s.c., intraven.	*Ibid.* 1913 *a*	+	Leishmania forms in blood and organs	Mice very weak, some died from infection. Spleen hypertrophied	Passages (3) successful
		(*d*) Mice	i.p.	*Ibid.* 1919	75 % +	,,	—	Flagellates produced in cultures
		(*e*) Mice	i.p.	Chatton, 1919	–	—	—	Cultures negative
		(*f*) Mice	i.p. (culture)	Laveran and Franchini, 1919 *a*	90 % +	Leishmania forms free and intracellular, and flagellates	Three died. Emaciation, diarrhoea. Liver and spleen hypertrophied	Virulence increased by passages
		(*g*) Mice	(Culture)	Nöller, 1920	–	—	—	—
		(*h*) Dog	per os	Fantham and Porter, 1915	+	—	—	—
		(*i*) Dogs	By placing dogs together with fleas	Wenyon, 1914	–	—	—	Dogs died from the effects of flea-bites

Species of flagellate	Host	Experimental animal	Mode of infection	Author	Result	Forms of parasites described in infected animals	Condition of infected animal	Remarks
4. *H. phlebotomi*	Sandfly	Dogs and guinea-pigs	s.c., i.p.	Laveran and Franchini, 1920	+	Leishmania forms free and intracellular, and flagellates	Symptoms of Kala-azar and Oriental Sore	—
5. *C. fasciculata*	Mosquito (*A. maculipennis*)	Mice and rats	?	*Ibid.* 1914, 1913 *a*	+	Leishmania forms	Symptoms of Oriental Sore	Parasites very rare. Successful passages
6. *C. melophagia*	Sheep-ked	Mice	(*a*) i.p. (cult.) (*b*) per os	*Ibid.* 1919 *a*, 1914 *b*	+	(*a*) Leishmania forms free and intracellular, and flagellates in blood and organs	—	(*a*) Virulence increased by passages
7. *C. tabani*?	*Tabanus socius*	Rats	i.p.	Wenyon, 1908	–	—	—	—
8. *H. pediculi*	*P. vestimenti*	Mouse	per os	Fantham and Porter, 1915 *a*	+	—	—	—
9. *H. muscae-domesticae*	Housefly	Mice and rats	i.p.	Franchini and Mantovani, 1915	+	Free leishmania forms in blood. Leishmanias in organs	Rat died "brusquement" after 3 months	Leishmania forms frequently with one nucleus. Rat's blood in culture produced "anaplasma" bodies which produced rare leishmania bodies in the liver of a mouse, when inoculated with it
10. *H. jaculum*	*Nepa cinerea*	(*a*) Mice	per os, i.p.	Fantham and Porter, 1915	+	Rounded forms in blood after a few hours. Leishmania forms and flagellates in organs	Mice weak, died, or killed *in extremis*	Parasites few
		(*b*) Sticklebacks	s.c., per os.	*Ibid.* 1915 *a*	+	Flagellates in blood, leishmania and flagellate forms in organs	Swelling at the site of inoculation	—
		(*c*) Toad	?	,,	+	—	—	—
		(*d*) Newt	per os	,,	?	—	—	Newt accidentally lost
		(*e*) Water-snake	?	,,	+	—	—	—
11. *C. gerridis*	Gerris	(*a*) Rana	i.p.	,,	+	Leishmania forms in blood, same and Crithidia in liver	—	Position of the "blepharoplast" (Kinetonucleus) varies and is not typical of Leishmania
		(*b*) Lacerta	i.p.	,,	+	—	—	
		(*c*) Mouse	i.p.	,,	+	—	—	
12. *H. stratiomyiae*	Stratiomys	Mice	per os	,,	+	Free leishmania forms in organs	Died after 5 days	

Summarising the results of Laveran and his collaborators, and Fantham and Porter, Laveran (1917) states that the experiments firmly establish the affinity between *Herpetomonas* (and *Crithidia*), on the one hand, and *Leishmania* on the other, an affinity which, from the phylogenetic point of view, is well recognised. Fantham (1915, 1915 *a*) goes a step further in his conclusions: he asserts that the experiments conducted by him and Porter, and Laveran and Franchini, prove that Leishmaniases are arthropod-borne herpetomoniases, and that these maladies have evolved mainly from insect flagellates. The experiments on artificial infection of vertebrates with these flagellates, according to this author, actually represent "leishmaniasis in the making."

Most of the flagellates with which Laveran and his collaborators dealt, and some with which Fantham and Porter worked, belong to insects which in nature are closely associated with some mammal, and it is known that some of these insects are capable of transmitting the haemo-flagellates to other vertebrate hosts, and infecting them, whilst others (*e.g.* the sand-fly) may eventually prove to be such intermediate hosts. On this account it is not surprising to find that the flagellates which parasitise the gut, and which may after all be insect stages of vertebrate haemo-flagellates, can produce infection when introduced into other vertebrates. In such cases no special adaptability is required.

Notwithstanding these facts, similar experiments repeated by other investigators produced negative results. Thus Chatton (1919) and Nöller (1920) repeated some of Laveran and Franchini's (1919) experiments with *H. ctenocephali*, but failed to find any traces of infection; similar experiments were made by Wenyon (1914) with the same flagellate, also with negative results. The last-named author also failed to produce any infection in rats inoculated with the flagellates of *Tabanus socius* (Wenyon, 1908).

As regards the pathogenicity of flagellates from insects which are not naturally associated with any vertebrate, this question is of more complex character. If such insect flagellates may become pathogenic to vertebrates when artificially introduced into them, we must assume that their power of adaptation is extraordinary, both as regards the time required for such adaptation in one generation, and as regards adaptation to the change of environment. This is the more surprising, if we take into account such protozoa as free-living amoebae which are frequently taken in by man and other animals, and pass through the whole digestive tract of the animal without becoming adapted to life in the latter, whereas closely allied forms of amoebae are found as obligatory parasites in the intestine of the same animal (cf. Wenyon, 1915; Dobell, 1919).

I shall now proceed with a description of my own experiments, and will return to the discussion of these questions later.

For my experiments I used the following flagellates: *Herpetomonas jaculum* from the water-scorpion (*Nepa cinerea*), *H. calliphorae* from the blue-bottle

fly (*Calliphora sp.*), and *Crithidia melophagia* from the sheep-ked (*Melophagus ovinus*). The animals experimented upon were mice, sticklebacks (*Gasterosteus aculeatus*), newts (*Molge vulgaris*) and frogs (*Rana temporaria*).

A. Experiments with Mice.

All the mice were inoculated intraperitoneally with the contents of the gut of insects infected with flagellates diluted with a physiological solution of sodium chloride. The animals were sacrificed after varying periods had elapsed, their blood being examined regularly till their death. After the animal was killed, cultures from its blood and organs—spleen and liver usually—in the *NNN* medium, and stained smears of the blood, peritoneal fluid, liver, spleen and, sometimes, bone-marrow and lungs were made. The blood and peritoneal fluid were also usually examined in the fresh condition.

I. *Mice inoculated with* C. melophagia.

Experiment 1. Mouse inoculated on October 19th, blood examined for two days with negative results. Sacrificed on October 21st. Stained smears of blood, peritoneal exudate, liver and spleen showed no parasites. Cultures made from the heart-blood, liver and spleen kept at 30° C. showed no parasites for 40 days.

Experiment 2. Mouse inoculated on October 19th. Blood examined with negative results till October 25th, when the animal was sacrificed. Stained smears (as preceding) showed no parasites. Cultures (as preceding) remained sterile for 36 days.

Experiment 3. Mouse inoculated on October 19th. Blood examined with negative results till October 29th, when the animal was sacrificed. Stained smears and cultures (as preceding) negative. Cultures examined for 32 days.

In experiments 1, 2 and 3 the three mice were inoculated with the contents of five "ked" guts; their condition was normal till death. The peritoneal fluid when examined showed numerous leucocytes.

Experiment 4. Mouse inoculated on July 15th. Blood examination during 25 days negative. Sacrificed August 9th. Stained smears of heart, blood, liver and spleen showed no parasites. Cultures from the blood and these organs kept at 24° C. remained sterile (27 days).

Experiment 5. Mouse inoculated on July 15th. Blood examination for 35 days negative. Sacrificed on August 19th. Stained smears and cultures (17 days) as in the preceding case—negative.

II. *Mice inoculated with* H. calliphorae.

Experiment 6. Mouse inoculated on August 9th. Sacrificed next day. Stained smears of blood, liver, spleen, kidney, bone-marrow, lung and peritoneal fluid were negative. Cultures from blood kept at 24° C. remained sterile (56 days).

Experiment 7. Mouse inoculated on August 9th. Sacrificed on the 19th. Stained smears (as preceding)—negative. Spleen culture showed no flagellates for eight days, when it became contaminated with bacteria.

In experiments 6 and 7 the peritoneal fluid showed numerous leucocytes.

III. *Mice inoculated with* H. jaculum.

Experiments 8 and 9. Two young mice inoculated on September 15th. Died next day. Peritoneal fluid and blood contained numerous bacteria. Blood cultures also showed bacteria.

Experiment 10. Young mouse inoculated on September 15th. Found dead on 17th. Not examined on account of decomposition.

Experiment 11. Mouse inoculated on October 26th. Sacrificed next day. Stained smears of blood, spleen and liver—negative. Peritoneal fluid showed numerous leucocytes. Blood cultures (at 30° C.) remained sterile for 11 days. The animal was in weak condition when killed.

Experiment 12. Young mouse inoculated on September 15th. Sacrificed on the 22nd. Blood examination till that date, negative. Smears of organs (as above)—negative. Blood cultures (13 days at 24° C.)—negative.

Experiment 13. Mouse inoculated on September 6th. Sacrificed on the 22nd. Blood examination till that date—negative. Smears of organs (as above)—negative. Blood cultures (13 days at 24° C.)—negative. For four days the mouse was in a weak condition, but recovered later.

Experiment 14. Mouse inoculated on October 26th. Sacrificed after one month (November 26th). Blood examination during that period revealed no parasites. Smears of blood, liver, spleen and peritoneal fluid—negative. Blood cultures kept at 24° C. remained sterile.

On the next day after inoculation the mouse was in weak condition, but soon recovered. It later developed gangrene on the tail, and examination *post mortem* showed a suppurative nodule in the liver, which, as I am told, is not uncommon in mice.

Experiment 15. Mouse inoculated on November 26th. After 3½ hours its blood and peritoneal fluid were examined fresh and stained. No parasites were found, but the exudate showed numerous leucocytes. The blood was regularly examined for 15 days, but showed no parasites. The mouse was sacrificed after 15 days; in smears of its organs no parasites could be found. Blood cultures kept at 24° C. remained sterile.

In the preceding experiments different doses of flagellates were inoculated into the mice. Nos. 8, 9, 10 and 12 received the contents of four *Nepa* guts each; Nos. 11 and 14—two each; No. 15—one gut.

As the experiments on mice show, there was no trace of flagellate infection in any of the cases recorded. Blood examinations were made at periods ranging from 3½ hours to 35 days with the same results. Cultures (at 24° C. and 30° C.) from the blood and organs of the infected animals examined in some cases for 56 days likewise failed to reveal any parasites.

B. Experiments with Fish.

I. *Sticklebacks* (Gasterosteus aculeatus) *fed on the flagellates of Nepa cinerea* (H. jaculum).

The contents of the gut of *Nepa* were examined for flagellates. If present, the gut was fed to the fish. It was always eaten immediately after being offered. Altogether 11 feeding experiments were conducted (each fish kept in a separate jar) varying according to the number of days they were fed, the number of *Nepa* guts they had eaten, and the length of time from the last meal to the date when they were sacrificed. For comparison, control fish were examined.

The examination of infected fish was conducted as follows. First the gill operculum was removed to expose the heart. Blood was then taken directly

from the heart either by means of a sterile pipette or by cutting the main artery (*Truncus arteriosus*) and allowing the blood from it to drop on a slide. Then, without injuring the alimentary canal (to avoid mixing its contents with other organs) the liver and spleen were removed and smeared on a slide. Films of the peritoneal fluid were also made. Lastly, the alimentary canal was totally removed and the stomach separated from intestine. The contents of the stomach and intestine, as well as the blood and peritoneal exudate, were examined both fresh in normal saline and in stained preparations.

Experiment 16 (VII). Fish fed on September 30th with one gut, October 1st, one gut, October 4th with two guts, one after another. Altogether it had four guts. *Killed two hours after last meal.* The insect gut was still undigested and nearly intact. The flagellates were quite motile in the stomach, but none were found in the intestine. The heart blood contained no flagellates, nor were any forms present in the liver, spleen and peritoneal fluid.

Experiment 17 (VIII). Fish fed on four guts (as preceding). *Killed* 3¾ *hours after last meal.* The insect gut was only partly digested. Motile flagellates were found in the stomach and a few already made their appearance in the intestine. No flagellates were found in the blood, peritoneal fluid, liver and spleen.

Experiment 18 (IX). Fish fed on three guts (as preceding, but only one gut on October 4th). *Killed five hours after last meal.* The insect gut was nearly digested. Few flagellates were found motile in the stomach, but none in the intestine. No forms found in the blood, exudate or liver and spleen.

Experiment 19 (IV). Fish fed on 12 guts (Sept. 17th one, Sept. 18th one, Sept. 20th two, Sept. 21st, 22nd, 23rd, 24th, 27th, 28th, 29th and 30th per one). *Killed five hours after last meal.* No visible traces of flagellates were found in the digestive tract, blood, exudate, liver and spleen.

Experiment 20 (III). Fish fed on nine guts (Sept. 17th, 18th, 20th, 21st per two, Sept. 22nd one). *Killed about five hours after last meal.* In the digestive tract flagellates were found with nuclei hardly visible, cytoplasm vacuolised, and shape of the body distorted. Apparently being digested. None were found in the blood, exudate and other organs.

Experiment 21 (XI). Fish fed on one gut (Sept. 6th). *Killed* 18 *hours after meal.* No live flagellates in fresh stomach contents. After the latter were stained, the flagellates were found to be apparently partly digested, their body being swollen, staining deeply and no inner structures being visible. There were no visible traces of the flagellates in the intestine. The insect gut was already wholly digested at this time. No forms of the flagellate were found in the blood, exudate and organs.

Experiment 22 (X). Fish fed on two guts containing an exceptionally large number of herpetomonads. *Killed* 18 *hours after the meal.* The insect gut was not yet quite digested and the alimentary canal contained some live flagellates, whilst others were found dead. None were found in the blood, exudate and organs.

Experiment 23 (I). Fish fed on ten guts (Sept. 16th two, Sept. 17th four, Sept. 18th, 20th per two). *Killed about* 24 *hours after last meal.* Insect gut wholly digested. No traces of flagellates in the digestive tract, blood and organs.

Experiment 24 (II). Fish fed on ten guts (Sept. 17th one, Sept. 20th two, Sept. 21st three, Sept. 22nd, 23rd per two). Results as in preceding.

Experiment 25 (VI). Fish fed on two guts (Sept. 17th and 18th). *Killed about* 48 *hours after last meal.* Results as in experiments 23 and 24.

Experiment 26 (V). Fish fed on seven guts (Sept. 17th, 18th, 20th, 21st, 22nd, 23rd, 24th per one). *Killed five hours after last meal.* The insect gut was nearly digested. In the

fresh contents of the stomach there were numerous dead flagellates, the bodies of which were distorted, the outlines and shape being very irregular and the cytoplasm vacuolised. In a stained preparation of the stomach contents in some of the flagellates the nucleus was still visible, in others it was diffused in the cytoplasm, and in some not visible at all. No flagellates were found in the blood of this fish, but smears of the spleen and liver contained several of them. This result was obviously due to carelessness on my part, as in this case the spleen and liver were separated from the intestine after the latter had already been removed from the fish. In this way the organs named were liable to be contaminated from the contents of the digestive tract. This is confirmed both by the fact that all the flagellates seen by me in the fresh contents of the fish-gut were already dead and had partly undergone digestion, and by the experiments adduced above in which the technique employed prevented such accidents from taking place.

In general, not only no harmful effect was observed from feeding the sticklebacks on the infected guts of *Nepa* for periods from one day to a fortnight, but they seemed to thrive on the food, being all the time very active and readily taking the guts whenever they were offered to them. Not one of the fish died from this food, and I may even say that the fish fed in this way were in better condition than the control fish kept in a tank with weeds and left to find food for themselves in the natural way.

These experiments show clearly that in the fish the flagellates are digested in the same way as any other food, and the fact that the flagellates remain alive for a considerable time only points to their vitality and power of resistance. This is not so surprising, taking into account that the flagellates are already adapted to life in the insect gut, the digestive juices of which do not differ materially from those in the higher animals.

These experiments also show that as long as any part of the insect gut remains undigested, thus protecting the flagellates enclosed in it from the action of the gastric juices, the flagellates in this part may remain alive. The action of the juices on the parasites is also exhibited in the fact that, whereas in the normal insect gut the flagellates are very numerous, very few can be

Table II.

Experiments on feeding sticklebacks on H. jaculum *from* Nepa cinerea.

No. of Experiment	Total No. of insect guts fed	No. of insect guts in last meal	Time from last meal to examination. Hours	Condition of food in the digestive tract of the fish (examined fresh)		Parasites in the blood, peritoneal fluid, liver and spleen of the fish
				Insect guts	Flagellates	
16	4	2	2	Undigested	Living	Absent
17	4	2	3½	Partly digested	„	„
18	3	1	5	„	Few living	„
19	12	1	5	„	None found	„
20	9	1	5	„	Dead	„
21	1	1	18	Digested	„	„
22	2	2	18	Partly digested	Few living	„
23	10	2	24	Digested	None found	„
24	10	2	24	„	„	„
25	2	1	48	„	„	„

found in the digestive tract of the fish, although practically the entire contents were examined in each case. A glance at Table II will show the correlation existing between the progress of digestion in the fish and the condition of the flagellates in its digestive tract, both depending also on the number of insect guts eaten by the fish (apparently the number of guts taken with the last meal is of greater importance than the total number, as a comparison between experiments 21 and 22 shows).

II. *Sticklebacks inoculated with* H. jaculum.

Experiment 27 (XVI). Fish inoculated intraperitoneally found dead next day. Death due to mechanical injuries, for immediately after inoculation the fish was seen to float on its side (probably, swim-bladder injured). Peritoneal fluid examined fresh, showed numerous bacteria and several motile flagellates. Stained smears of blood, liver and spleen showed no forms of the flagellates.

Experiment 28 (XVIII). Fish inoculated intraperitoneally. Killed two days after inoculation. Peritoneal fluid showed plenty of motile flagellates; blood and organs negative. In the liver bacteria were visible.

Experiment 29 (XIX). Fish killed four days after intraperitoneal inoculation. The fish looked weak, its movements were slow. *Post mortem* showed signs of a haemorrhage on the genital glands, probably caused by injection. Fresh blood showed bacteria; in the peritoneal exudate numerous bacteria and one or two living flagellates were visible. The exudate also contained numerous leucocytes. Stained preparations of the blood, liver, spleen, revealed no traces of flagellates.

Experiment 30 (XVII). Fish killed six days after intraperitoneal inoculation. The fish looked quite normal before it was killed. In fresh peritoneal fluid bacteria were visible. No traces of the flagellates were found in the blood and organs.

Experiment 31 (XV). Fish inoculated subcutaneously died in half an hour after the operation, evidently from mechanical injuries (the bases of the fins and tail immediately became white, probably from penetration of air introduced by injection). An examination of the fluid from under the skin showed motile flagellates.

Experiment 32 (XIV). Killed 24 hours after subcutaneous inoculation. A slight swelling appeared on one side of the body, but disappeared when dissected. The fluid taken from under the skin showed no parasites, but it contained numerous leucocytes and bacteria. The liver and spleen also showed only a few bacteria, and no flagellates were found in the blood.

Experiment 33 (XIII). Killed two days after subcutaneous inoculation. Fresh fluid from under the skin showed no flagellates, but several of them were recovered from the peritoneal fluid, which contained numerous leucocytes, some of which had phagocytised flagellates enclosed in them, together with bacteria.

Blood and spleen negative; in the liver bacteria were visible.

Experiment 34 (XII). The fish was left alive after subcutaneous inoculation and seemed to be quite normal for three weeks, after which it was placed in a tank with other fish.

The experiments on inoculation of sticklebacks with *H. jaculum* show that no infection whatever is produced by the flagellates thus introduced into the fish. The most careful examination of the body fluids and organs did not reveal the presence of any forms of the parasites, except in the site of inoculation, or of any lesions produced by them, whereas the bacteria naturally occurring in *Nepa* and introduced into the fish together with the flagellates, seem to find

a footing there, being nearly always present either free or in leucocytes in the blood, peritoneal exudate and organs. These experiments have, however, again shown the extent to which the insect flagellates are capable of retaining their vitality in the body of the fish under conditions unusual to them. It is seen that they can be found alive in the peritoneal cavity and subcutaneous fluid of the fish for two to four days, but they disappear altogether on the sixth day, being probably phagocytised, as on several occasions I was able to find leucocytes that contained flagellates in degenerate condition within them.

A summary of these experiments is given in Table III.

Table III.

Experiments on inoculation of sticklebacks with H. jaculum.

No. of experiment	Mode of inoculation	Date of inoculation	Interval between inoculation and examination	Results of examination of fresh blood and body fluids	Results of examination of stained smears	Remarks
27	i.p.	28 x. 20	24 hrs (died)	In perit. fluid *motile flagellates* and bacteria. Blood—negative	Blood, liver and spleen—negative	Death due to mechanical injuries
28	—	—	2 days (killed)	In perit. fluid *motile flagellates*. Blood—negative	Blood, liver and spleen—negative. Liver contained bacteria	—
29	—	—	4 days (killed)	In perit. fluid *single flagellates*, numerous bacteria. Blood—negative	Blood, liver and spleen—negative. Perit. fluid contained numerous leucocytes	Fish looked weak. *Post mortem* genitalia showed signs of haemorrhage. (Mechanical injury)
30	—	—	6 days (killed)	In perit. fluid *no* flagellates, numerous bacteria. Blood—neg.	Negative	Fish quite normal
31	s.c.	26 x. 20	30 min. (died)	Subcutaneous fluid contained *motile flagellates*	—	Died from penetration of air introduced by injection
32	—	—	24 hrs (killed)	In subcutaneous fluid *no* flagellates; numerous leucocytes and bacteria	Negative. Spleen and Liver contained bacteria	Slight swelling on one side of the body
33	—	—	2 days (killed)	In subcut. fluid *no* flagellates. In perit. fluid several *flagellates* free and phagocytized, and bacteria	Negative. Liver contained bacteria	—
34	—	—	—	—	—	Remained quite normal for 3 weeks, when it was transferred to a tank with other fish

C. Experiments with Amphibians.

I. *Newts* (Molge vulgaris) *inoculated with, and fed on,* H. jaculum.

(*a*) Newts inoculated intraperitoneally. November 11th.

Experiment 35. Newt killed after 24 hours. No forms of the flagellates found in fresh peritoneal fluid and blood, nor in stained smears of the same, and liver and spleen.

Experiment 36. Newt killed after two days. Results as above. Peritoneal fluid contained numerous leucocytes.

Experiment 37. Newt killed after four days. Results as preceding.

Experiment 38. Newt killed after five days. Results as preceding.

Experiment 39. Newt was left alive.

(*b*) Newts fed on *H. jaculum* introduced by a pipette *per os*.

Experiment 40. Newt killed after 24 hours. Examined contents of the alimentary tract, blood, liver, spleen, peritoneal fluid. Nowhere were any traces of the flagellates visible.

Experiment 41. Newt left alive.

The experiments on newts show that in their organism the flagellates are apparently very soon disposed of, no traces of them being visible even after 24 hours. There was no change in their condition, and two newts inoculated intraperitoneally and *per os* respectively remained living, showing no signs of infection.

II. *Frogs* (Rana temporaria) *inoculated with* H. jaculum.

Experiment 42. Young frog inoculated into the dorsal lymph-sinus on November 26th. Killed after 24 hours. Examination of fresh blood and fluid from the lymph-sinus, and of stained blood, sinus fluid, liver and spleen revealed no traces of parasites.

Experiment 43. Young frog inoculated on the same day intraperitoneally. Results as in preceding.

Experiment 44. Adult ♀ frog inoculated into the dorsal lymph-sinus on the same day. Killed after 19 days. Blood examination during the period preceding death—negative. *Post mortem* results as in Nos. 42 and 43. Blood-cultures from this frog kept at 24° C. showed no parasites for more than a month.

The experiments with frogs thus also produced negative results, although the mode of inoculation through the lymph-sinus in two cases afforded an easy and natural point of access to the blood-stream of the frog.

III. OBSERVATIONS ON THE VITALITY OF SOME INSECT FLAGELLATES.

The degree of vitality of some flagellates when exposed to abnormal conditions is shown in some of the experiments already recorded. As these experiments have demonstrated, the flagellates can remain alive in the intestine of fish for five hours, and in some cases (experiment 22) for 18 hours, resisting the action of the digestive juices. When injected subcutaneously or intraperitoneally into fish, they may be found alive in the peritoneal fluid for four days. I have also kept insect flagellates living in sealed drops with a physiological solution of sodium chloride and with sterile nutritive bouillon at different temperatures. The results were as follows:

Contents of the gut of the sheep-ked (*Melophagus ovinus*) infected with *Crithidia melophagia* diluted with normal saline were kept at room temperature and at 30° C. In the portion that was placed at 30° C. the flagellates lived only one day, but those that were kept at room temperature lived seven days. No multiplication was observed, and the flagellates gradually lost their motility.

Contents of the gut of the water-scorpion (*Nepa cinerea*) infected with *Herpetomonas jaculum* were placed at room temperature in saline and in slightly alkaline nutritive bouillon. In both cases the flagellates remained alive for five days. It was observed that towards the end of that period their movements became slower, many had become rounded off, retaining their flagella, others had swellings on different parts of their body.

Regarding the vitality of *C. melophagia* Flu (1908) mentions that it is possible to keep them alive in normal saline only for two hours, and in serum for eight hours at room temperature. In an ice chest they remained alive for six days. According to Porter (1909) the same flagellates remain alive for several hours at room temperature. Georgéwitch (1910) kept his flagellates living in drops of serum for several days.

CONCLUSIONS.

In my experiments on artificial infection of mice with *Crithidia melophagia*, *Herpetomonas jaculum* and *H. calliphorae*, I was unable to confirm the results obtained by Laveran and his collaborators, having found no traces of infection or of the presence of any forms of flagellates in the animals experimented upon. Whether this is due to difference in methods or to some other cause, it is difficult to tell. The most remarkable feature of the experiments of these observers is that positive results were produced so invariably, whereas in my experiments made on fifteen mice which were most carefully examined at different periods of their life and *post mortem*, and in all cases tested by cultural methods, the results were always negative. This difference cannot be due to the authors mentioned having used flagellate cultures for inoculation, as they started experimenting with cultures only since 1919; up to that time they produced positive results by inoculating flagellates directly from the guts of the insects and otherwise. As it is, my experiments, which are not so numerous and varied as those discussed, although not disproving the experiments described by Laveran and his collaborators, at any rate clearly show, together with the experiments of Wenyon (1908, 1914), Chatton (1919) and Nöller (1920), that artificial infection with insect flagellates requires further study and the results already recorded do not permit as yet of forming general conclusions as to the pathogenicity of insect flagellates, and their relation to Leishmaniasis.

In connection with this, I should like to add that in some of the experiments discussed the results are difficult to understand. For instance, Franchini and Mantovani's (1915) experiments with *H. muscae-domesticae* are quite incomprehensible. The authors state that blood cultures from a rat inoculated with these flagellates produced only "anaplasma" bodies. These bodies, when reinoculated into a mouse, gave rise to leishmania forms. The "anaplasma," as we know it, is merely a structureless granule within red cells, which stains red with Romanowsky stains, and it is still questionable whether it is in reality an organism at all, although some recent workers definitely assert that they

are protozoa (cf. Lignières, 1919; Di Domizio, 1919). Whatever the case may be, there are no grounds for connecting the "anaplasma" with the flagellates.

In the experiments of these authors and Laveran and his colleagues reference is frequently made to leishmania forms with only a single nucleus. It must be very doubtful if these can be regarded as such. In the examination of smears of organs, in experiments of this kind, only undoubted leishmania forms should be considered. According to these authors, leishmania forms are also produced by infecting mice with *C. melophagia* (Laveran and Franchini, 1914 *b*, 1919 *a*). As Nöller's (1919, 1919 *a*, 1920) observations have proved this flagellate to be a trypanosome (*T. melophagium*), its inoculation into mice would be likely to produce in the latter trypanosomes, and not leishmanias.

The experiments of Fantham and Porter (1915, 1915 *a*) are of especial interest in this respect. These authors have made experiments on artificial infection working chiefly with flagellates of insects not associated normally with any vertebrate animal. They claim to have proved that insect flagellates may be successfully inoculated into and fed to different warm- and cold-blooded animals. The flagellates become pathogenic to these animals and produce in them symptoms resembling Kala-azar and other leishmaniases.

Fantham (1915, 1915 *a*) concludes from these experiments that "the occurrence of natural herpetomonads in invertebrates must not only be acknowledged, but it must be allowed that they may become pathogenic, when introduced into vertebrates," thus apparently extending the results of the experiments discussed to all insect herpetomonads.

I have repeated some of the experiments recorded by Fantham and Porter with the negative results already described. In the case of infection of fish, my experiments were much more numerous and varied than those recorded by the authors named. In inoculating frogs, the site of injection (lymph-sinuses) would seem to afford the easiest point of access for the flagellates into the blood stream of the host. Notwithstanding these facts, I have utterly failed in producing even the slightest sign of infection in these animals, and have never found any forms of the flagellates introduced into them which would suggest infection.

The conclusions of Fantham (1915, 1915 *a*) already quoted, and the more general conclusion that leishmaniases are "arthropod-borne herpetomoniases" are very interesting from the theoretical point of view, and it is quite possible that later discoveries will prove this to be a fact, and not merely a hypothesis.

The facts available at present, however, do not in my opinion permit one to assert that the natural herpetomonads in insects, especially in those not associated with vertebrates, may become pathogenic, when introduced into the latter, as the author suggests.

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AN ANNOTATED LIST OF THE ANIMAL PARASITES OF FOXES[1].

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Few people have any conception of the rapid growth and the importance of the new industry of raising black and silver foxes for their fur. According to Dearborn, 1917, the first profitable fox ranch was established in the Canadian Province of Prince Edward Island in 1894. This ranch, the forerunner of a remarkable industry, was stocked with two pairs of silver foxes, a rare and beautiful colour phase of the common red fox found in nearly all of the United States and Canada.

Until 1910, the methods of growing of these foxes was kept a profound secret and practically "monopolised" by a few Prince Edward Islanders. Now there are many farms throughout Canada and the Northern United States and some foreign countries, notably Japan. Literally millions of dollars are invested, and prime breeding stock sells for many times the value of a high grade horse. In spite of the very heavy decline in prices of furs, prime pelts of the silver foxes are to-day worth from $500 to $1200 each.

Until very recently practically no attention from an economic view-point has been paid to the animal parasites of foxes. They have been regarded as of merely general zoological interest, and that mainly from the systematic side. Now, with the rapid development of the fur farming industry, this condition is rapidly changing, for it is clear that intensive studies of any factors affecting the health or the quality of the fur of foxes are of great economic importance.

Data regarding these points are not easy to obtain. This is in part due to the widespread ignorance regarding the nature of parasitic diseases. In part it is due to the fact that to-day the average grower of silver foxes depends for his largest profits on the sale of breeding stock and hence is loath to admit that he has any trouble from disease. Indeed, it is commonly stated that foxes are remarkably free from disease. However true this may be of the animals in nature, there is no reason to hope that the condition will long prevail among the domesticated forms.

In general it might be supposed that foxes would be subject to the same parasites as are dogs and other Canidae. How true this is we have not at present sufficient data to judge. Certain it is that many parasites which infest

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dogs have not yet been reported for foxes. On the other hand, several fox parasites are thought to occur exclusively in these animals.

In the following list are included such animal parasites as have been reported for foxes, together with notes on their occurrence, and probable pathogenic significance.

PROTOZOA.

There are very few records of the occurrence of parasitic protozoa in foxes. While several serious protozoal diseases are known to occur in dogs, they are fortunately prevalent chiefly in the tropics and in sub-tropical regions. Successful fox fur farming is limited to the cooler zones, a long cold season being an important factor in producing suitable fur growth.

Trypanosoma brucei Plimmer and Bradford, 1879. This trypanosome, the well-known causative organism of the tsetse-fly disease "Nagana" of cattle has been experimentally transmitted to the fox by Yakimoff (1917). *Trypanosoma gambiense* has also been inoculated successfully into experimental foxes by Laveran (1915).

In spite of the extensive study devoted to the trypanosomes, there does not seem to be any record of their occurrence in the fox in nature.

Trichomonas sp.—Dr W. L. Chandler informs me that he has found in Michigan a species of *Trichomonas* occasional in foxes. While it is the usual tendency to regard the members of this genus as harmless commensals, recent studies, notably those of Hadley (1916) and Tyzzer (1920), indicate that under some conditions they may be highly pathogenic.

Isospora bigmenina (Stiles, 1891). (Synonyms: *Coccidium bigeminum*, Stiles, 1891; *Diplospora bigemina* (Stiles) Wasielewski, 1904.) In foxes from three separate ranches we have found a coccidium which agrees fairly closely with the species found by Stiles in the dog. The rounded somewhat ovoid cysts have a double-contoured wall and measure on the average 30μ by 25μ. Both single and two-spored oocysts are found in the fresh faeces.

Weidman (1915) has discussed the finding of what appears to be this same coccidium in the faeces of two swift foxes from the Western United States, which were kept in the Philadelphia Zoological Gardens. "Both foxes when in isolation showed diarrhoea, the one more marked than the other. In the former the oocysts were in great numbers and in about a week the animal died. The second fox, on the other hand, passed very small numbers of cysts, spontaneously recovered, and after isolation for several weeks was returned to exhibition, the faeces no longer containing oocysts." Autopsy of the dead fox disclosed a most marked haemorrhagic and ulcerative enteritis involving both small and large parts of the bowel. Within the ulcers were found mature naked protozoa, and upon the mucosal surface double-walled oocysts corresponding to those found in the faeces.

As the oocysts found in the fox averaged considerably larger than those reported by Stiles for the dog Weidman considered them sufficient to constitute a new variety, *canivelocis*. The organism should be studied in greater detail.

in order to determine definitely its relation to the species described by Stiles.

Theileria sp. Yakimoff and his associates have reported (1917) the finding of an undetermined species of *Theileria* in the blood of foxes in Russian Turkestan.

CESTODA.

Some thirty species of cestodes have been reported as occurring in foxes. When the synonomy is considered this list is reduced to less than half. In none of the cases, in so far as I have found, is there any reference to the effects upon the fox. The pathogenicity of some, the species which affect other hosts than the fox, is well known.

The species reported for the fox are listed alphabetically below, together with notes on synonomy and on the host species where available.

Bothriocephalus similis Krabbe, 1865.

In *Vulpes lagopus*, Greenland.

Cysticercus vulpis (Gmel. 1790) Zed. 1803.

(Synonym: *Taenia vulpis* Gmel. 1790.)

In *Vulpes*, Europe.

Diphyllobothrium latum (Linn. 1758) Luehe, 1910.

(Synonyms: *Taenia lata* Linn. 1758; *Bothriocephalus latus* Bremser, 1819; *Dibothriocephalus latus* Luehe, 1899.)

Occurs rarely in the common fox of Europe (Braun; Railliet)

Dithyridium elongatum (Blumberg, 1882) Raill. 1893.

(Synonyms: *Cysticercus elongatus* Blumberg, 1882; *Cysticercus bailleti* Railliet, 1885.)

This larval form, resembling a plerocercoid except that it possesses four suckers, occurs in the peritoneal or pleural cavity, free or encysted in dogs and cats. Neumann (1896) reports finding a great number in the peritoneal and pleural cavities, as well as beneath the serous membrane of the liver and lung of a fox. Allessandri (1907) also reports it for the fox.

Neumann presents evidence indicating that these forms may be erratic larvae of *Mesocestoides lineatus*, which he commonly found in the intestines of the same animals.

Mesocestoides canis-lagopodis (Rud. 1810) Luehe 1894.

(Synonyms: *Taenia canis-lagopodis* Rud. 1810; *Ptychophysa canis-lagopodis* Loennb. 1896.)

From *Vulpes lagopus*.

Mesocestoides lineatus (Goeze, 1782) Braun, 1898.

(Synonyms: *Taenia lineata* Goeze, 1782; *Taenia pseudo-cucumerina* Bailliet, 1863; *Ptychophysa lineata* Hamann, 1885.)

Various writers report this as from the common fox of Europe. Some of these records relate to the following species, *M. litteratus* Batsch.

Mesocestoides litteratus (Batsch, 1786) Dolley, 1894.

(Synonyms: *Taenia litterata* Batsch, 1786.)

Type host, European fox.

Monodoridium utriculifera Walter, 1866.

(Synonyms: *Taenia utriculifera* (Walters, 1866) Linstow, 1878; according to Stossich, 1896 = *Mesocestoides litteratus*.)

Type host *Vulpes vulpes*.

Multiceps multiceps (Leske, 1780) Hall, 1910.

(Synonyms: *Taenia coenurus* Kuchenmeister, 1853; *Cystotaenia coenurus* Leuckart, 1863; *et al.* For details of the extensive synonomy see Hall, 1910.)

Various writers have reported the adults of this species for the blue fox, *Vulpes lagopus*, and for the red fox *Vulpes vulpes*. While Hall questions all of these records there is no apparent reason for so doing.

Taenia crassiceps Rud. 1819.

Type host a fish, *Gadus merluccius*. The record for the fox, by Olt and Strase, 1914, is due to confusion with *Taenia crassiceps* Zeder.

Taenia crassiceps (Zeder, 1800) Rud. 1810.

(Synonyms: *Alyselminthus crassiceps* Zeder, 1800.)

Type host *Vulpes vulpes*, Europe, "Also reported for *Vulpes melanogaster*" (Stiles and Hassall).

Taenia hyperborea Linstow, 1905.

Vulpes lagopus, in E. Greenland.

Taenia ovata Molin, 1858.

Vulpes vulpes, and *Vulpes lagopus*.

Taenia pisiformis (Bloch, 1780) Gmel. 1790.

(Synonym: *Taenia serrata* of various authors, but not as used by Goeze, 1782.)

Reported by Cobbold (1786) and various other writers for common fox of Europe.

Taenia polyacantha Leuckart, 1856.

Vulpes vulpes, Germany.

Tetrabothrius vulpis Blainv. 1828.

Type host, fox.

TREMATODA FROM FOXES.

Ascocotyle longa Ransom, 1920.

Intestine of *Vulpes lagopus*, National Zoological Park, Washington, D.C.

Ascocotyle nana Ransom, 1920.

Same data as for *A. longa.*

Conchosomum alatum (Goeze, 1782) Railliet, 1896.

(Synonyms: *Alaria vulpis* Schrank, 1788; *Festucaria alata* Schrank, 1790; *Fasciola alata* Rud. 1793; *Distoma alatum* Zed., 1800; *Holostomum alatum* Nitzsch, 1819; *Hemistomum alatum* Dies, 1850; *Diplostomum alatum* Parona, 1894.)

According to Olsson (1876) from *Vulpes alopax* and *V. lagopus.*

Reported for various hosts in Europe, Egypt, Brazil and New South Wales.

Cotylophallus venustus Ransom, 1920.

Intestine of Alaskan fox, *Vulpes lagopus*, National Zoological Park, Washington, D.C.

Echinostoma trigonocephalum (Rud. 1803) Cobbold, 1860.

(Synonyms: *Fasciola trigonocephala* Rud. 1802; *Distoma trigonocephalum* Rud. 1809.)

Reported by Stossich (1892) for *Vulpes vulpes*, intestine.

Heterophyes heterophyes (Siebold, 1852) Stiles and Hassall, 1900.

(Synonym: *Coenogonimum heterophyes.*)

Looss (1902) records it doubtfully from fox.

Metorchis conjunctus (Cobbold, 1860) Looss, 1899.

(Synonym: *Distomum conjunctum* Cobbold, 1860.)

"Numerous examples in the liver of the American red fox, *Canis fulvus*"—Cobbold (1860).

Opisthorchis felineus (Rivolta, 1884) Blanchard, 1895.

(Synonym: *Distomum conus* Gurlt, 1831, nec Creplin, 1825.)

Gall ducts of fox, as well as of dogs, cats and man.

Opisthorchis noverca Braun, 1902.

Not found in foxes. Statements as to its occurrence are based on McConnell's erroneous assumption that his specimens from man in India were identical with Cobbold's *Distomum conjunctum.*

Pseudamphistomum truncatum (Rud. 1819) Luehe, 1909.

(Synonyms: *Amphistoma truncatum* Rud. 1819; *Distomum conus* Creplin, 1825; *Metorchis truncatus* Looss, 1899.)

In gall ducts of fox, dog, cat, seals, etc.

NEMATODA.

Ancylostoma caninum (Ercolani, 1859) Looss.

(Synonyms: *Strongylus trigonocephalus* and *S. tetragonocephalus* Rud. 1808; *Dochmius balsamoi* Parona and Grassi, 1877; *Uncinaria trigonocephala* Raill. 1885; *Ankylostomum tubaeforme* Linstow, 1885.)

There are numerous European records of the occurrence of this hookworm in foxes, but I do not know of any explicit American record. The adult hookworms from the fox which I have at hand are all of *Uncinaria polaris*, but I am not warranted in concluding definitely that all of the hookworm eggs which I have noted in faeces examinations are of this species.

Ancylostoma caninum is common in cats and dogs in this region. Hall reports it in 23 out of 67 dogs, or 34 per cent. at Detroit, Michigan. My records for Minnesota dogs are not extensive enough to justify a statement of percentages, I have found it in ten out of 30 cats examined. It is a significant fact that it is a common practice of fox growers to use cats as foster mothers of fox puppies if the vixen is unable to provide for them.

Belascaris marginata (Rud. 1802) Leiper, 1907.

(Synonyms: *Ascaris marginata* Rud. 1802 *pro parte.*)

This common ascarid of dogs frequently occurs in foxes and is the cause of serious trouble in the case of the pups. By most growers it is considered the most common, or practically the only "worm" of foxes, owing doubtless to the fact that the worms are to be found in the droppings. My examinations would lead me to think it less frequent than are hookworms. The latter were found in 26 out of 30 samples from four different farms, while ascarids were present in but six.

Belascaris vulpis (Frölich, 1789) Railliet and Henry, 1911.

(Synonyms: *Ascaris vulpis* Frölich, 1789; *Ascaris triquetra* Schrank, 1790.)

Railliet and Henry (1911) recognise the *Ascaris vulpis* of Frölich from *Vulpes vulpes*, as a valid species closely related to *Belascaris marginata*. The spicules are of the same length as in the latter species, but the caudal extremity of the body is excavated in a gutter-like manner (creusée en gouttière) and almost triangular with caudal wings well developed.

It is to be noted that among 200 ascarids from 25 Massachusetts dogs, Walton (1916) found two which he regarded as *Ascaris triquetra* Schrank (= *B. vulpis*).

Crenosoma semiarmatum Molin, 1861.

(Synonyms: *Strongylus decoratus* Creplin, 1847; *Liarhynchus vulpis* Dujardin, 1845.)

Reported by Bremser, Dujardin and Creplin, as found in the lungs and trachea of *Vulpes vulpes*.

Dioctophyme renale (Goeze, 1782) Stiles, 1901.

(Synonyms: *Ascaris visceralis* Gmelin, 1789; *Strongylus gigas* Rud., 1802; *Eustrongylus gigas* Diesing, 1851.)

The giant kidney-worm was reported for both the European and the common American fox, by Rudolphi, 1819.

Eucoleus aerophilum (Creplin, 1839) Duj. 1845.

(Synonym: *Trichosoma aerophilus* Creplin, 1839.)

Trachea of *Vulpes vulpes*.

Filaria vulpis Comper.

Rudolphi questions whether this worm, reported by P. Comper as from the abdomen of a fox, was not merely a wandering ascarid from the intestine.

Habronema grimaldiae Seurat, 1915.

From stomach and intestine of the Algerian fox, *V. vulpes atlantica*.

Ollalanus tricuspis Leuckart, 1865.

From the tunic of the stomach of the cat; reported also for the fox.

Rictularia affinis Jägerskiöld.

Type specimens from the Egyptian fox; Seurat (1915) reports it for the Algerian fox, *V. vulpes atlantica*.

Spirocerca subaequalis Seurat, 1915.

From stomach of Algerian fox.

Spiroptera sanguinolenta Rud. 1819.

(Synonyms: *Strongylus lupi* Rud. 1809; *Filaria sanguinolenta* Schneider, 1866.)

In tumours in the stomach and oesophagus of various Canidae, including foxes. Embryos in the blood.

Spirura gastrophila (Mueller, 1895).

Seurat (1918) found this species in the Algerian fox.

Strongyloides longus (Grassi, 1885).

Intestine of fox, Russia. Romanovic (1914).

Strongylus vulpis Rud. 1819.

Bremser reported finding in the mesenteric glands of the fox a worm which Rudolphi lists with others under the heading "Entozoa vel Generis dubii, vel fictitia." It remains unknown. Obviously it cannot belong to the genus *Strongylus* as now delimited.

Trichinella spiralis (Owen, 1835) Railliet, 1895.

The fox is susceptible to infestation by *Trichinella spiralis*. Grüner (1916) describes trichinosis in captive wild animals including *Vulpes lagopus*.

Trichocephalus depressiusculus Rud. 1809.

(Synonyms: *Trichocephalus vulpis* Frölich, 1789; *Mastigodes vulpis* Zeder, 1803.)

I have found this in 12 per cent. of the foxes examined. It is reported frequently in the literature as occurring in these hosts.

Trichosoma plica Rud. 1819.

(Synonym: *Calodium plica* Duj. 1845.)

In the bladder of *Vulpes vulpes*.

Uncinaria criniformis (Rud. 1809) Railliet, 1899.

(Synonyms: *Ascaris criniformis* Goeze, 1782; *Strongylus criniformis* Rud. 1809; *Uncinaria stenocephala* Raill. 1884.)

Commonly found in European foxes and other Canidae. Also found in the Arctic fox *V. lagopus*.

Uncinaria polaris Looss, 1911.

Type host *Vulpes lagopus* from the National Zoological Gardens, Washington, D.C. Stiles (1902), who sent the material to Looss, states that it was the cause of an outbreak of uncinariasis among the Arctic foxes of the Zoological Garden.

Riley and Fitch (1921) have reported this species as very common in three out of four silver fox ranches examined, and as the undoubted cause of loss, not only through death of young stock, but through affecting the quality of the fur of infested animals.

Uncinaria vulpis Frölich, 1789.

Though the genus *Uncinaria* is now generally accepted, this, the type species, is listed by Looss as a *species inquirenda*.

LINGUATULINA.

Linguatula serrata Frölich, 1789.

(Synonyms: *Taenia rhinaria* Pilger, 1802; *Pentastoma taenoides* Rud. 1819.)

The adult of this problematic arthropod occurs in the nasal cavities of the fox, as well as of the dog, wolf, and a variety of animals.

ACARINA.

Demodex folliculorum (Simon, 1842).

This mite, the cause of the exceedingly stubborn follicular mange of dogs is known to occur, though rarely, in the fox. Apparently Gros (1845) was the first to definitely list the fox as a host. Since his time there have been a number of references, but nothing specific in the literature.

Sarcoptes scabiei vulpis (Fürstenberg, 1861) Raill.

Sarcoptic mange is widely distributed among foxes and fox farmers regard it as one of the parasitic diseases that are most to be feared because of its high degree of contagiousness. Since the disease was discovered, a thorough-going quarantine and inspection of all imported foxes has been maintained.

Fürstenberg and also Braun have called attention to the fact that the variety occurring in the fox is transmissible to man. Weydemann (1897) records a case where a fur dealer and his entire family became infested from a

mangey weasel skin which was subsequently found to harbour great numbers of what he identified as *Sarcoptes vulpis*.

Dermanyssus gallinae, the common red mite of poultry is said by Wood (1917) to be conveyed by foxes, skunks, weasels, etc.

IXODOIDEA.

Many species of ticks occur on a variety of hosts. The following species have been taken from the fox:

Amblyomma americanum (Linn. 1758).
Amblyomma tuberculatum Marx.
Dermacentor variabilis (Say, 1821).
Haemaphysalis bispinosa intermedia Warburton and Nuttall, 1909.
Haemaphysalis cinnabarina punctata (Canestrini and Fanzago, 1877).
Haemaphysalis inermis Birula, 1895.
Haemaphysalis leachi (Audouin, 1827) Neumann, 1897.
Ixodes canisuga Johnston, 1849.
Ixodes hexagonus Leach, 1815.
Ixodes marxi Banks, 1908.
Ixodes ricinus (Linnaeus, 1746 and 1758) Latreille, 1804.
Rhipicephalus sanguineus (Latreille, 1804).

MALLOPHAGA.

Trichodectes quadraticeps Chapman, 1887, has as its type host the California gray fox, *Urocyon cinereoargenteus*.

Trichodectes vulpis Denny, 1842 (Synonym: *T. micropus* Giebel, 1874) is from the common European fox.

SIPHONAPTERA.

Pulex irritans Linnaeus, 1858. *Vulpes* sp.

Pulex pallidus Taschenberg, 1880. *Vulpes niloticus*.

Ctenocephalus canis (Curtis, 1826) Baker, 1904. *Vulpes lagopus*, *V. vulpes*, *Urocyon cinereoargenteus*.

Ceratophyllus melis Curtis, 1832, "sur le Renard" Raill.

Chaetopsylla vulpes (Motscherlsky, 1840) Baker, 1905. *Vulpes vulpes*.

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NOTE.

Since the above paper was in print I have received two important publications bearing upon the topic of animal parasites in foxes.

The long awaited part of the *Index Catalogue of Medical and Veterinary Zoology* which deals with round worms is now available as Bulletin No. 114 of the Hygienic Laboratory of the U.S. Public Health Service. This will prove an invaluable aid to students of the Nematoda.

A paper by M. C. Hall, 1920, on "Intestinal Parasites found in Eighteen Alaskan Foxes" (*North American Veterinarian*, I. 123–124) reports on the examination of eighteen foxes from Saint George Island, Alaska. "Of the eighteen foxes, eight were infested with ascarids, ten with *Mesocestoides*, and one with *Taenia*, and one fox had a number of dipterous larvae, probably from fly-blown flesh. Some of the ascarids have been examined and found to be *Toxascaris*, possibly *T. limbata*, and all of them may belong to the same species. The infestations were not heavy, the largest number being twelve."

A surprising feature of the findings is the absence of hookworms. "This suggests that the island is free from this worm which is a serious pest to foxes elsewhere."